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THE BOTANICAL GAZETTE

Editor: JOHN M. COULTER

OCTOBER 1921

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A MONTHLY JOURNAL EMBRACING ALL DEPARTMENTS OF BOTANICAL SCIENCE

EDITED BY

JOHN M. COULTER

With the assistance of other members of the botanical staff of the University of Chicago

Issued October 15, 1921

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THE

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SEXUAL DIMORPHISM IN CUNNINGHAMELLA

ALBERT F. BLAKESLEE, J. LINCOLN CARTLEDGE, AND DONALD S. WELCH

(WITH ONE FIGURE)

Introduction

HETEROTHALLIC AND HOMOTHALLIC FORMS

In 1904 (1) it was shown that the mucors can be classified into two main groups according to their ability to produce zygospores from the sowing of a single spore. Species which are able to form sexual spores by the conjugation of branches from the same plant were called homothallic, since the mycelia appeared to be sexually alike; those which were able to form sexual spores only by the interaction of different plants were called heterothallic, since the mycelia taking part in conjugation appeared to be sexually different. The terms homothallic and heterothallic were used instead of hermaphroditic and dioecious because at the time they were first suggested our knowledge of sexuality in the mucors did not seem to warrant unreservedly accepting the idea of a strict sexual dimorphism in these forms, although such a dimorphism was strongly indicated by the interaction which had just been discovered between plus and minus races.

In later publications (5, 6) the desirability was pointed out of extending the use of the terms homothallic and heterothallic to signify the type of sexual differentiation in all gametophytes, in contrast with the terms homophytic and heterophytic suggested

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In later publications (5, 6) the desirability was pointed out of extending the use of the terms homothallic and heterothallic to signify the type of sexual differentiation in all gametophytes, in contrast with the terms homophytic and heterophytic suggested

for sporophytes. It was not expected that these terms would supplant the more familiar words hermaphroditic and dioecious. They may be found useful in bringing about greater accuracy in sexual terminology, and in emphasizing the inconsistency of calling a form like *Marchantia* dioecious and a form like the common lily hermaphroditic, when the two belong to the same sexual type.

Evidence for sex intergrades in heterothallic species

It is well known that sex intergrades are relatively frequent in sporophytic plants like the willow and hemp, which are commonly classified as dioecious. Similar sexual abnormalities, therefore, have been expected and sought for in heterothallic mucors ever since heterothallism was discovered in these forms in 1903. The fact that no race of a heterothallic mucor[1] has been found by the writers which, if it gave any sexual reaction at all, behaved otherwise than as a plus *or* a minus, indicates that sex intergrades in these forms are at best extremely rare. It is true that a number of investigators have reported findings which they have interpreted as opposed to the existence of a strict sexual dimorphism in the bread molds and related forms. Despite the fact that their conclusions were in harmony with our expectations based upon the condition in higher forms, the instances of supposed sex intergrades in heterothallic species are either isolated observations of two conjugating filaments which seem to originate from the same hypha, or have been supported by experimental evidence open to criticism. The inadequacy of the evidence has been pointed out in earlier publications (**4**, **7**, **8**), but it seems appropriate to mention two examples more or less typical of their kind. The first case is cited by Miss McCormick (**15**), and is illustrated by a figure showing a partially matured zygospore with the suspensor on one side arising from a filament which curves over and connects with the filament from the suspensor on the other side. In reply to an inquiry in regard to this zygospore Miss McCormick has written that after the

[1] The peculiar homothallic mycelium produced by regeneration of the germ tube and at times produced from the germination of spores in the germ sporangium in *Phycomyces* (**3**) is a temporary condition only, and apparently should more properly be considered a mixochimera of plus and minus protoplasm, as Burgeff (**13**) suggests, than as a sexually constant race.

drawings were made the homothallic strand was lost in an attempt to make a permanent mount of the fresh material. So far as we are aware, such a condition as Miss McCormick figures has not been described elsewhere for *Rhizopus* since 1903, when heterothallism was first discovered in the mucors. Inasmuch as an enormous number of zygospores of *Rhizopus* must have been observed more or less closely during this time, since it is a common type for laboratory study (Miss McCormick herself [16] reports having examined over 2000 in her cytological investigations in this species), it appears reasonable that in an isolated instance of this kind, the filaments from the two sides of the zygospore which appeared to be connected may in fact have been separate, but the place of separation obscured by overlying hyphae. That it is unsafe to judge of the thallic condition of a species from the hyphal connections is shown by experience with a class of students who were studying *Rhizopus* shortly after heterothallism had been discovered in other mucors, but before it had been demonstrated for this species. They were asked to find cases in which both the suspensors originated from branches of the same filament. A number of cases were found in which the two suspensors actually seemed to be connected, but in every instance there were one or more overlying filaments which would render the condition open to doubt by a critical observer.

The second case is a paper by Namyslowski (17), in which he throws doubts upon heterothallism in the whole group of the mucors. His experimental evidence comes from isolating single spores of *Rhizopus* and sowing the resulting mycelia on bread. The appearance of zygospores in fourteen out of forty-six such single spore cultures led him to conclude that his *Rhizopus* was homothallic. As has already been pointed out (7), the facts that six of these cultures were destroyed by bacteria and that thirteen more were devoid of even sporangia and hence probably also infected with bacteria, rendered it probable, to one familiar with pure culture methods, that the zygospores which Namyslowski obtained in part of his cultures from the sowing of a single spore actually might have arisen through interaction with the opposite sex which had gained access to these cultures through infection. This explanation seemed later confirmed by the isolation of the two sexual strains

from zygosporic material which NAMYSLOWSKI kindly sent to one of us. NAMYSLOWSKI (18), however, still believes, upon evidence which we have criticized, that heterothallic species have been shown capable of producing homothallic zygospores.

The two examples given are typical of less careful observations. Although cases of homothallism in heterothallic species on a priori grounds were to be expected, we have never found them ourselves, and could not feel that the reports of them by other investigators could stand critical examination. It reminded one of the reports of the birth of a full black negro baby from pure white parents which from time to time have appeared in literature and been passed on by rumor, but which have in no case been confirmed by students of human heredity.

BURGER ON CUNNINGHAMELLA

The condition outlined was the situation in the early part of 1919, when BURGER announced the finding of hermaphroditic as well as "pseudo-heterothallic" strains in *Cunninghamella* and *Syncephalastrum*. At the same time report came from one of the laboratories of the Department of Agriculture of a strain of *Rhizopus* which would form zygospores with both plus and minus test strains of this species. As to the *Rhizopus*, it was found upon inquiry that this particular strain had died out, and that after all it had not shown the capacity of conjugating with both the opposite sexes. BURGER'S paper on sexuality in *Cunninghamella* (14) presents the most extensive evidence which has yet appeared for sex intergrades in any heterothallic mucors. Although his arguments from the data presented seemed open to some criticism, his publication made the genus *Cunninghamella* the most likely source known for sex intergrades, the investigation of which would have considerable genetic interest. Recently published studies by one of us (11) had shown that races with plus and races with minus tendencies can arise by mutation from a homothallic species, and that such a race may cease to form zygospores and take on the appearance of a heterothallic species. It seemed worth while, therefore, to look for races with homothallic tendencies among heterothallic species, in view of BURGER'S paper. Accordingly, a rather extensive study of the interaction of strains

has been made for four species of *Cunninghamella*, the details of which will be given later. Since they offer no support to BURGER'S conception of hermaphroditism in the genus, and since his cultures were allowed to die out before his final results were published, making it impossible for his material[2] to be retested, it is necessary to subject both his experimental technique and conclusions to searching criticism in lieu of other means of judging of the correctness of a statement which runs counter to the experience of most careful workers on the Mucorineae. BURGER'S paper will be considered before discussing the results of this investigation.

BURGER found great irregularity in the sexual behavior of races of *C. bertholletiae*. While some races were consistently either plus or minus in reaction, others appeared to react both as plus and minus with properly chosen test strains. Certain races seemed to form a sexual triangle. His race *A*, for example, would form zygospores with *B*, race *B* would form zygospores with *C*, race *C* would form zygospores with *A*, and the family triangle was complete.

BURGER'S conclusions are based primarily upon tests with twenty-six[3] races of *C. bertholletiae*. Since he says "authentic cultures of *C. bertholletiae* and *C. elegans* were obtained from Holland," and later credits us with having sent the only race of *C. elegans* which he used in his tests, there is little doubt that his race no. 21 of *C. bertholletiae* is identical with the no. 213 which we secured from the Centralstelle, and of which we sent a subculture to the Harvard laboratory with *C. elegans* shortly before BURGER used the strains in his investigations. In addition to these two races, he used the plus and minus strains of *C. echinulata* and of *Mucor V*, which had also been sent by us to the Harvard laboratory. The sexual races of these two species were contrasted with all his twenty-six races of *C. bertholletiae*, but without finding any "imperfect hybridization" reactions. The race of *C. elegans* and six races of *C. bertholletiae* were individually contrasted with the remaining races of a collection consisting of twenty-six races of *C. bertholletiae*, five races of *C. echinulata* (including our plus and minus strains),

[2] Except his race no. 21, which will be discussed later.

[3] In two places in the text (probably through error), his race no. 25 is called *Mucor V* minus.

and plus and minus strains of *Mucor V* and the plus strain of *C. elegans*. The positive and negative results are assembled in a table. The sexual condition seemed to BURGER so hopelessly confused that he was led to the following conclusions contained in his summary:

1. In *Cunninghamella* there does not exist sexual dimorphism.

2. *C. echinulata* plus and minus, or *Mucor V* plus and minus as separated by BLAKESLEE, are unable to form progametes or gametes when contrasted with any one of twenty-six cultures of *C. bertholletiae*.

3. Many of these cultures of *C. bertholletiae* were able to form zygospores when contrasted with certain other cultures of this same species.

4. There exists a selective power in some strains to form zygospores with certain other strains. This condition of pseudoheterothallism cannot be explained at present.

5. There exists a condition in some strains which might be called hermaphroditism.

6. In none of the hermaphroditic strains did branches of the same hyphae conjugate.

7. Zygospores were produced only when two strains were contrasted whose gametes were compatible.

It will be well to examine this summary to see whether the rather sweeping conclusions are warranted from BURGER'S own data, assuming for the moment that these data are not open to criticism. The results of his contrasts are more readily compared if his table be rearranged as shown in table I. The six testers of *C. bertholletiae* are placed at the top, together with the plus race of *C. elegans* and of *Mucor V*, which were also used as testers. On the side, grouped according to sex, are placed the twenty-six races with which the testers were contrasted; *H* stands for imperfect hybridization, *Z* for zygospores. If the latter is inclosed in parenthesis, it indicates the occurrence of zygospores in a contrast where they would not be expected on the basis of a strict sexual dimorphism. No grades are given in table I, since none are presented in the original paper.

The sexual behavior of the twenty-six races of *C. bertholletiae* shown in the table I is not so badly mixed as even BURGER himself was apparently led to believe from his method of analyzing the data. He says: "Nos. 1 and 2 have always remained constantly

plus, while nos. 4–6, 12, 15, 18, 19, 22–26 were always minus, nos. 3, 7–11, 13, 14, 16, 17, 20, 21, ... however, have reacted with both the so-called plus and minus strains." This is a curious conclusion, that nos. 1 and 2 are constantly plus because they

TABLE I

REARRANGEMENT OF DATA IN BURGER'S TABLE I: *Cunninghamella bertholletiae*, 26 RACES (1–26); NUMBER OF COMBINATIONS POSSIBLE, 325; NUMBER OF COMBINATIONS MADE, 135; ABERRANT COMBINATIONS, 6; "PSEUDOHETEROTHALLIC HERMAPHRODITIC RACES," 3 TO 8; Z STANDS FOR OCCURRENCE OF ZYGOSPORES, H FOR OCCURRENCE OF "IMPERFECT HYBRIDIZATION" REACTION; PARENTHESES INDICATE THAT REACTION IS ABERRANT ON BASIS OF SEXUAL DIMORPHISM

Races contrasted	9 plus or plus and minus	10 plus	14 plus or plus and minus	34 [*C. elegans* plus]	33 [V plus]	21 minus or plus and minus	7 minus or plus and minus	3 minus or plus and minus
Plus or plus and minus 9...	.....	O	O	O	O	Z	Z	Z
Plus 10...	O	.....	O	O	O	Z	Z	Z
Plus or plus and minus 14...	O	O	.....	O	O	Z	Z	Z
Plus or plus and minus 16...	O	O	(Z)	O	O	Z	Z	Z
Plus 17...	O	O	O	O	O	Z	Z	Z
Plus or plus and minus 20...	(Z)	O	(Z)	O	O	Z	Z	Z
Plus 1...	O	O	O	O	O	Z	O	O
Plus 2...	O	O	O	O	O	Z	O	O
Plus 11...	O	O	O	O	O	O	O	Z
Minus or plus and minus 3...	Z	Z	Z	H	O	(Z)	O	.....
Minus or plus and minus 7...	Z	Z	Z	O	O	(Z)	.....	O
Minus 8...	Z	Z	Z	H	O	O	O	O
Minus 12...	Z	Z	Z	H	O	O	O	O
Minus or plus and minus 13...	Z	Z	Z	H	O	(Z)	O	O
Minus or plus and minus 21...	Z	Z	Z	H	O	.....	(Z)	(Z)
Minus 4...	Z	O	Z	O	O	O	O	O
Minus 5...	Z	O	O	O	O	O	O	O
Minus 6...	Z	O	O	O	O	O	O	O
Minus 15...	Z	O	O	O	O	O	O	O
Minus 18...	O	Z	O	O	O	O	O	O
Minus 19...	O	Z	O	O	O	O	O	O
Minus 22...	O	Z	O	O	O	O	O	O
Minus 23...	O	Z	O	O	O	O	O	O
Minus 24...	O	O	O	H	O	O	O	O
Minus 25...	O	O	O	H	O	O	O	O
Minus 26...	O	O	O	H	O	O	O	O
[V minus] 32...	O	O	O	H	Z	O	O	O

produced zygospores with a hermaphrodite (no. 21) and with no other race; while no. 11 is listed among those which have reacted with both the so-called plus and minus strains when it formed zygospores only with no. 3, which need not be considered other than as a good minus. BURGER further believed that there were twelve hermaphrodites, since he lists this number, including no. 11 among

those reacting with both plus and minus strains. Referring to table I, it will be seen that in only eight contrasts are zygospores found where under a strict sexual dimorphism they would not be expected. Two of the eight are duplicates, leaving only six different contrasts showing aberrant reactions. It is not necessary, however, to consider more than three races hermaphroditic to account for the aberrant results. These three hermaphrodites may be variously chosen. Race no. 21 has three aberrant reactions, which is the largest number shown by any race. Both races nos. 14 and 20 show two aberrant reactions each, and may be chosen with no. 21 to make up the three hermaphrodites. Since nos. 14 and 20 are both assumed to be hermaphrodites, the reaction between them ought not perhaps to be credited to both of these races. However the credit of aberrancy is adjusted between nos. 14 and 20, race no. 21 remains the one which gives the largest number of aberrant reactions, and therefore of all the twenty-six races it is the one most surely shown by BURGER'S data to be a hermaphrodite. This no. 21 is the same as our no. 213, and is the only one of the twenty-six races which it has been possible to reinvestigate. Its sexual behavior will be discussed more fully later.

Conclusion no. 1 of BURGER'S summary that in *Cunninghamella* there does not exist sexual dimorphism would seem too sweeping a statement in view of the fact that in *Mucor* and *Absidia*, which are predominantly heterothallic, forms are known, such as *Mucor heterogamus* (which with other similar species has been placed by some workers in the genus *Zygorhynchus*), and *Absidia spinosa*, which are homothallic. Races of two other species of *Cunninghamella* reported upon in the paper under discussion gave no evidence of hermaphroditism, and in consequence the data presented warrant the conclusion at most in reference to a single species. That in this single species three out of twenty-six races showed, in 135 out of a possible 325 contrasts, six reactions which were interpreted as indicating hermaphroditism, would render the species in the same class with the willows and others of the flowering plants called dioecious. That sexual dimorphism, strictly speaking, does not exist in higher plants is strongly suggested by past observations and experimentation, but the term sexual dimorphism is

currently applied to the so-called dioecious condition in forms like the willow, despite the familiar exceptions.

Conclusion no. 2, that the sexual races of *C. echinulata* and *Mucor V* as separated by us are unable to form progametes with any of the twenty-six races of *C. bertholletiae* studied, is too sweeping a statement, and will be shown later to be incorrect. In place of "are unable to form" should have been written "have not been observed to form" progametes.

The statements of fact in conclusions nos. 3, 4, and 7 are what one could make in regard to a heterothallic species. Conclusion no. 5, that a condition of hermaphroditism exists in some strains, seems somewhat opposed to the fact brought out in no. 6, that these hermaphrodites do not themselves take part in conjugation when growing alone in pure cultures, "a fact which indicates that this species is not homothallic," according to BURGER. "Homothallic" it will be remembered is a term used by us to indicate a hermaphroditic condition in gametophytes. The line of reasoning is as follows: some strains are hermaphrodites, in none of the hermaphroditic strains did branches of the same hyphae conjugate, therefore the species is not hermaphroditic.

Earlier in the paper the fact that the stock tubes containing the individual twenty-six races did not produce zygospores under nutrient and temperature conditions favorable for their formation showed according to BURGER "that the cultures were pure and not a mixture of strains." On the contrary, BURGER'S own data show that lack of zygospore formation cannot be a proof of freedom from mixture of strains. Table I makes the matter clear. The minus race no. 4 fails to form zygospores with the plus race no. 10. If nos. 4 and 10 were mixed in a tube culture, therefore, they would not be expected to form zygospores, and yet the plus component (no. 10) of this mixture would form zygospores with the minus races 3, 7, 8, etc., while the minus component (no. 4) would form zygospores with the plus races nos. 9 and 14. The tube containing the mixture suggested would be able to conjugate, therefore, with both plus and minus strains, and such a reaction is BURGER'S proof of hermaphroditism in *Cunninghamella*. Table I shows that eighteen out of the twenty-six races could be mixed to form twenty different

combination pairs capable of reacting with both plus and minus races. If all of the 325 possible contrasts had been made between the twenty-six races instead of only the 135 actually attempted, it is probable that a considerably larger number of pairs of races, capable when mixed of producing zygospores with both plus and minus races, would be evident. So far as the data of BURGER go, however, they are sufficient to show that absence of zygospores in a culture cannot be offered as proof that it is not a mixture of strains; and to indicate that infection, if it occurred, rather than the existence of pseudoheterothallic hermaphrodites, might be the cause of zygospores in cultures where they would not be expected on the basis of sexual dimorphism.

BURGER believed he had eliminated the possible objection that his cultures had been mixed by making several single spore cultures from each of the strains nos. 9, 3, and 21, and obtaining zygospores whenever such cultures from one of these strains were contrasted with those from either of the other two strains. The test, on the face of it, may appear to be a critical one, and in fact if only these three strains had been kept in cultivation they would now afford an opportunity of critically retesting data upon which BURGER'S theories are based. Since, however, these cultures were destroyed before the publication of his paper in which their peculiar behavior is described, it will be necessary to depend upon circumstantial rather than upon direct evidence. As seen from table I, nos. 9 and 3 may be considered good plus and minus races, and in consequence should be expected to give reactions when grown together. In consequence, interest centers rather in strain no. 21. This race it will be remembered gave the most aberrant reactions, and together with nos. 14 and 20 is able to account for all the evidence that can be brought forward in support of BURGER'S theory of pseudoheterothallism. No 21 is predominantly minus and so should be expected to give reactions with the plus strain no. 9. The abnormal reaction, therefore, is between nos. 21 and 3. The surprising thing about these tests is that apparently there were no controls. Each of the three single spore cultures of no. 3 were contrasted against each of the four single spore cultures of no. 21,

but nothing was said about control contrasts between the subcultures of no. 3, nor of contrasts between the subcultures of no. 21, nor is mention anywhere made of uninoculated controls to discover what the danger might be from air infection of spores of the opposite sexes. For aught we know, single spore subcultures of any race might have appeared to produce zygospores when contrasted together at the time BURGER made his single spore cultures, which was apparently at the end of his series of contrasts with the twenty-six races. Neither in these single spore culture contrasts nor in any of the others is the abundance of zygospores graded. A single zygospore or a limited number which might make the investigator suspicious of mixture of strains in his stock culture or of infection in his contrast culture apparently have been classified as of equal value with our grades *A* and *B*.

In a previous paper (**12**) attention was called to the peculiar danger of air borne infection of *Cunninghamella* when forms of this genus had previously been grown in the laboratory. *Cunninghamella*, it may be remembered, was first described as an *Oedocephalum*, a hyphomycetous genus with exogenous spores, but was later (**2**) shown to be a heterothallic mucor by the isolation of its sexual races and their combination to form zygospores. It has already been shown that another investigator who found zygospores in his cultures after planting the mycelia from single spores was apparently misled into a theory of hermaphroditism for *Rhizopus* on account of unsuspected infection of his cultures with sexual races of the same species. It seems reasonable to suspect that BURGER has fallen into a similar error, since he gives no evidence to the contrary, rather than to believe he has discovered a sexual condition unparalleled in the experience of other critical workers.

There are a number of perhaps minor matters in the body of BURGER'S paper, such as the use of the terms neutral and zygotactic, to which objection might be made. Enough has been said, however, to indicate that his data do not inevitably lead to his main conclusion of pseudoheterothallic hermaphroditism in *Cunninghamella*.

BURGER'S CONCLUSIONS COMPARED WITH NEW DATA

It will be remembered that of the cultures used by BURGER, *Cunninghamella echinulata* plus and minus, *C. elegans* plus, *Mucor V* plus and minus, and his race no. 21 of *C. bertholletiae* were obtained from us. These races are still running, and it has been possible therefore to compare their behavior with the observations of BURGER on the same material.

The second conclusion in his summary, to the effect that neither the sexual strains of our *C. echinulata* nor those of our *Mucor V* are able to form progametes with any one of twenty-six cultures of *C. bertholletiae*, is contrary to our experience. Table II shows

TABLE II

"IMPERFECT HYBRIDIZATION" BETWEEN RACES OF *Cunninghamella bertholletiae* AND *Mucor V* PLUS AND MINUS; *Mucor V* PLANTED 4:00 P.M., 11/19/19; *C. bertholletiae* PLANTED 11:00 A.M., 11/20/19; RECORDS TAKEN 2:00 TO 4:00 P.M., 11/22/19; NUTRIENT NO. 380 (BURGER'S OATMEAL AGAR); c AND d INDICATE GRADES OF IMPERFECT HYBRIDIZATION; O INDICATES ABSENCE OF OBSERVED REACTION

C. bertholletiae	Plus races						Neutral races		Minus races					
	217	227	268	234	464	456	215	452	266	457	459	213	241	180
Mucor V plus...	O	O	O	O	O	O	O	O	c	c	O	d	c	O
Mucor V minus..	c	d	c	c	c	O	O	O	O	O	O	O	O	O

the results of contrasts between the sexual races of *Mucor V* and testers from the collection of races of *C. bertholletiae* grown on oatmeal agar made up according to BURGER'S method of preparation. The majority of the races (including no. 213, which is BURGER'S no. 21) showed "imperfect hybridizations" with the opposite sex of *Mucor V*. The nutrient chosen does not appear to be the best for the reaction, but was used to make the conditions of the experiment so far as possible comparable with those reported in the paper under discussion. "Imperfect hybridization" between *Mucor V* plus and our race no. 213 has been obtained on other nutrients, but the reaction with this particular race has never been strong and might readily have been missed had we employed a less successful method of observation (12).

Our old test races of *C. echinulata* (nos. 885 and 886) are able to form "imperfect hybridization" reactions with a number of the races of *C. bertholletiae*, although no sexual reaction between them and our race no. 213 has been observed.

Our race no. 213, which is the same as BURGER'S no. 21 and is the strain which furnished the strongest evidence for his theory of pseudoheterothallic hermaphroditism, has been tested against eighty-eight other races of the same species obtained from Brazil nuts from various localities. In all these tests it has reacted, if at all, only as a minus. In BURGER'S experience, although predominantly a minus, it produced zygospores in three combinations with the seventeen other minus races, a total of 17.5 per cent of the contrasts between it and other minus races. If it had reacted in the same manner we should have expected it to produce zygospores with a minimum of eleven of our sixty-eight other minus races. As a matter of fact, it showed reactions with none of these minus races. That so great a difference really exists between our minus strains and those studied by BURGER seems unlikely.

BURGER seems not to have observed the imperfect sexual reactions between races of *C. bertholletiae* which failed to carry through to zygospore formation. Partly for this reason perhaps, despite his own evidence already adduced to the contrary, he failed to appreciate the fact that absence of zygospore formation in a culture is not a proof of its freedom from mixture with strains of the opposite sex. The imperfect reactions in *C. bertholletiae* will be discussed later. In our experience the plus race no. 465 forms only imperfect reactions with the minus race 457. In consequence, when these two races are planted mixed in a Petri culture in contrast with the plus race no. 217 and the minus race no. 459, a triangular reaction has been obtained, as shown in fig. 1, where the mixture is represented as forming zygospores with *both* the plus race no. 217 and the minus race no. 459, while the latter two are also forming zygospores together. Although we have obtained the triangular reaction shown in fig. 1, which BURGER considered a proof that sexual dimorphism does not exist in *Cunninghamella*, we know in this case that the reaction is due to a mixture of strains and not to pseudoheterothallic hermaphroditism. BURGER'S

conclusions, therefore, are not justified from his own data, and the few races which it has been possible to retest from among those studied by him have shown either reactions which he considered impossible or have failed to show the reactions which he found and upon which his theory of pseudoheterothallic hermaphroditism in *Cunninghamella* was based. It must be emphasized, however, that despite the necessity for considering the evidence for sex intergrades in heterothallic mucors open to serious criticism, there is no proof at hand that such intergrades do not exist. A somewhat detailed consideration of the evidence for them in *Cunninghamella* has been given to indicate a few of the dangers into which even one with some experience with cultural methods is likely to fall. The data already published (10) and to be presented in the following pages show that sex intergrades must be extremely rare in the mucors, and place the burden of proof on observers who think they have found evidence for their occurrence.

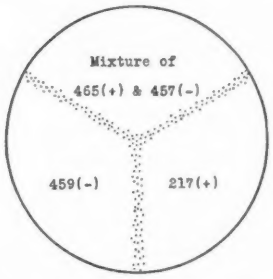


FIG. 1.—Diagram representing Petri dish culture: at lower right and left were planted respectively plus and minus races 217 and 459 which are forming zygospores (represented by dots at line of contact between them); in upper third was planted a mixture of plus and minus races 465 and 457 which fail to form zygospores with each other, but form them with the respective opposite sexes 459 and 217.

New data on Cunninghamella

Tests of the sexual condition in *Cunninghamella* were made with 202 races of four species; forty-two races of *C. elegans*, eighteen races of *C. echinulata*, eighty-nine races of *C. bertholletiae*, and fifty-three races of a species as yet unidentified.[4] The method of running the

[4] The discrepancy between the number of races given here and that listed in a previous publication (10) is due to the separation of *Cunninghamella A* from the other species and the omission of four races from the tables on account of infection in the stock tubes, because of incomplete records or for other reasons. All told, including tests with other genera, a considerably larger number of contrasts has been made with *Cunninghamella* than is reported.

gross cultures to obtain the races to be investigated, as well as the detailed methods of making contrasts between them has been described in a previous publication (**12**) and need not be repeated here. Table III gives the origin of the different races used in the tests. Samples of different types of soil were taken from different stations, chiefly near Cold Spring Harbor, and were the source of races of *C. elegans* and *C. echinulata*. Brazil nuts furnished both *C. bertholletiae* and *C. echinulata*, as well as the undetermined species *A*. All the gross cultures were given a serial number preceded by the letter *T* or *H*. The individual nuts in these cultures were indicated by capital letters, and the same was done for the spots on the soil and bread cultures from which transfers were made. In some cases more than a single transfer was made from an individual nut, as is shown by nos. 737 and 738. Generally more than a single race was isolated from each gross culture which showed fruits of the fungus sought, since, as table III shows, sexually distinct races are frequently present in the same gross culture. Undoubtedly among our numbered races some are duplicates, but duplication would probably not have been avoided if only a single race had been taken from each purchased collection of nuts.

More races of a single species were taken from *T*117 than from any other gross culture. From this culture, however, both plus and minus sexes were obtained, and the various races of the same sex are far from all being duplicates, as may be seen by comparing the records of nos. 732, 733, and 739, shown in table VII *A*. Despite the facts that the opposite sexes were frequently found to be present in the same culture and that the gross cultures were run at a temperature favorable for sexual reproduction, no zygospores of *Cunninghamella* in gross culture were found. Their absence may be due to the relatively meager growth of the fungus under the conditions in gross cultures.

The tests with the different species may be considered separately. The individual and mean grades were assigned as already described (**10**, **12**). For the most part, individual contrasts were made only once, since it seemed more profitable to obtain somewhat roughly graded records of a relatively large number of separate

TABLE III

LIST OF RACES OF *Cunninghamella* INVESTIGATED SHOWING RACE NUMBER; SPECIES, WHETHER *C. bertholletiae* (*C. berth.*) *C. echinulata* (*C. ech.*), *C. elegans* (*C. eleg.*), OR THE UNDETERMINED SPECIES *C.A.*; IN CASE OF BRAZIL NUTS, PLACE IN WHICH NUTS WERE PURCHASED IS INDICATED.

Race no.	Species	Culture no.	Substratum	Locality represented	Plus	Neutral	Minus
179..	C. berth.	H_1 E	Brazil nuts	Huntington, N.Y.	x	.....	.....
180..	C. berth.	H_1 B	Brazil nuts	Huntington, N.Y.	.....	.....	x
181..	C. A.	H_1 C	Brazil nuts	Huntington, N.Y.	x	.....	.....
182..	C. A.	H_1 E	Brazil nuts	Huntington, N.Y.	.....	.....	x
183..	C. berth.	H_1 B	Brazil nuts	Huntington, N.Y.	.....	.....	x
184..	C. A.	H_1 G	Brazil nuts	Huntington, N.Y.	.....	.....	x
185..	C. berth.	H_1 A	Brazil nuts	Huntington, N.Y.	.....	.....	x
186..	C. berth.	H_1 D	Brazil nuts	Huntington, N.Y.	.....	.....	x
187..	C. A.	H_2 C	Brazil nuts	Huntington, N.Y.	.....	.....	x
188..	C. A.	H_2	Brazil nuts	Huntington, N.Y.	.....	.....	x
189..	C. berth.	H_2 B	Brazil nuts	Huntington, N.Y.	.....	.....	x
190..	C. A.	H_2 B	Brazil nuts	Huntington, N.Y.	x	.....	.....
191..	C. A.	H_2 C	Brazil nuts	Huntington, N.Y.	x	.....	.....
192..	C. berth.	H_2 C	Brazil nuts	Huntington, N.Y.	.....	.....	x
193..	C. A.	H_2 E	Brazil nuts	Huntington, N.Y.	x	.....	.....
213..	C. berth.	.....	.....	"Centralstelle," Holland	.....	.....	x
214..	C. berth.	T_{12} C	Brazil nuts	New York City	.....	.....	x
215..	C. berth.	T_{13} Y	Brazil nuts	New York City	.....	x	.....
216..	C. berth.	T_{27} A	Brazil nuts	Huntington, N.Y.	.....	.....	x
217..	C. berth.	T_{38} A	Brazil nuts	Oyster Bay, N.Y.	x	.....	.....
218..	C. berth.	T_{38} D	Brazil nuts	Oyster Bay, N.Y.	x	.....	.....
219..	C. berth.	T_{38} E	Brazil nuts	Oyster Bay, N.Y.	.....	.....	x
220..	C. berth.	T_{39} A	Brazil nuts	Oyster Bay, N.Y.	.....	.....	x
221..	C. berth.	T_{39} B	Brazil nuts	Oyster Bay, N.Y.	.....	.....	x
222..	C. berth.	T_{39} D	Brazil nuts	Oyster Bay, N.Y.	.....	.....	x
223..	C. berth.	T_{40} A	Brazil nuts	Oyster Bay, N.Y.	.....	.....	x
224..	C. A.	T_{40} D	Brazil nuts	Oyster Bay, N.Y.	.....	.....	x
225..	C. A.	T_{40} B	Brazil nuts	Oyster Bay, N.Y.	.....	.....	x
226..	C. berth.	T_{40} C	Brazil nuts	Oyster Bay, N.Y.	.....	.....	x
227..	C. berth.	T_{40} E	Brazil nuts	Oyster Bay, N.Y.	x	.....	.....
228..	C. berth.	T_{48} A	Brazil nuts	Hicksville, N.Y.	.....	.....	x
229..	C. ech.	T_{13} G	Brazil nuts	New York City	x	.....	.....
232..	C. berth.	T_{50} F	Paradise nuts	New York City	.....	.....	x
233..	C. berth.	T_{51} A	Brazil nuts	New York City	.....	.....	x
234..	C. berth.	T_{51} B	Brazil nuts	New York City	x	.....	.....
245..	C. A.	T_{51} E	Brazil nuts	New York City	x	.....	.....
236..	C. ech.	T_{51} H	Brazil nuts	New York City	x	.....	.....
237..	C. berth.	T_{52} A	Brazil nuts	New York City	.....	.....	x
238..	C. ech.	T_{52} C	Brazil nuts	New York City	x	.....	.....
239..	C. A.	T_{52} D	Brazil nuts	New York City	.....	.....	x
240..	C. berth.	T_{53} B	Brazil nuts	Worcester, Mass.	.....	.....	x
241..	C. berth.	T_{53} C	Brazil nuts	Worcester, Mass.	.....	.....	x
242..	C. A.	T_{53} D	Brazil nuts	Worcester, Mass.	x	.....	.....
243..	C. berth.	T_{54} A	Brazil nuts	Washington, D.C.	.....	.....	x
244..	C. berth.	T_{54} B	Brazil nuts	Washington, D.C.	.....	.....	x
245..	C. berth.	T_{55} A	Brazil nuts	Brooklyn, N.Y.	.....	.....	x

TABLE III—*Continued*

Race no.	Species	Culture no.	Substratum	Locality represented	Plus	Neutral	Minus
246..	C. berth.	T55 B	Brazil nuts	Brooklyn, N.Y.	.....	.....	x
247..	C. berth.	T55 F	Brazil nuts	Brooklyn, N.Y.	.....	x	.....
248..	C. ech.	T66 A	Brazil nuts	New York City	x	.....	.....
249..	C. berth.	T66 B	Brazil nuts	New York City	.....	x	.....
250..	C. ech.	T66 C	Brazil nuts	New York City	.....	.....	x
252..	C. berth.	T67 A	Brazil nuts	New York City	.....	.....	x
253..	C. berth.	T67 C	Brazil nuts	New York City	.....	.....	x
254..	C. berth.	T68 A	Brazil nuts	Brooklyn, N.Y.	.....	.....	x
255..	C. ech.	T68 A	Brazil nuts	Brooklyn, N.Y.	x	.....	.....
256..	C. A.	T68 B	Brazil nuts	Brooklyn, N.Y.	.....	.....	x
257..	C. A.	T68 C	Brazil nuts	Brooklyn, N.Y.	.....	.....	x
258..	C. berth.	T68 D	Brazil nuts	Brooklyn, N.Y.	.....	.....	x
259..	C. A.	T68 E	Brazil nuts	Brooklyn, N.Y.	x	.....	.....
260..	C. A.	T68 E	Brazil nuts	Brooklyn, N.Y.	x	.....	.....
261..	C. A.	T73 A	Brazil nuts	New York City	x	.....	.....
262..	C. berth.	T73 B	Brazil nuts	New York City	.....	.....	x
265..	C. ech.	T44 B	Soil	Cold Spring Harbor	.....	.....	x
266..	C. berth.	T50 F	Paradise nuts	New York City	.....	.....	x
267..	C. A.	T52 D	Brazil nuts	New York City	x	.....	.....
268..	C. berth.	T52 D	Brazil nuts	New York City	x	.....	.....
269..	C. A.	T68 C	Brazil nuts	Brooklyn, N.Y.	.....	.....	x
270..	C. A.	T27 B	Brazil nuts	Huntington, N.Y.	.....	.....	x
271..	C. berth.	T38 B	Brazil nuts	Oyster Bay, N.Y.	x	.....	.....
272..	C. A.	T68 D	Brazil nuts	Brooklyn, N.Y.	.....	.....	x
273..	C. A.	T73 C	Brazil nuts	New York City	x	.....	.....
274..	C. berth.	T73 C	Brazil nuts	New York City	.....	.....	x
275..	C. berth.	T74 E	Brazil nuts	New York City	.....	.....	x
372..	C. berth.	T76 B	Brazil nuts	New York City	.....	.....	x
373..	C. berth.	T76 C	Brazil nuts	New York City	.....	x	.....
446..	C. berth.	.....	Brazil nuts	Brooklyn, N.Y.	.....	.....	x
447..	C. berth.	T74 C	Brazil nuts	New York City	.....	.....	x
448..	C. berth.	T75 A	Brazil nuts	New York City	.....	.....	x
449..	C. berth.	T79	Brazil nuts	New York City	.....	.....	x
450..	C. berth.	T80 B	Brazil nuts	New York City	.....	x	.....
451..	C. berth.	T80 E	Brazil nuts	New York City	.....	.....	x
452..	C. berth.	T81 B	Brazil nuts	Brooklyn, N.Y.	.....	x	.....
453..	C. berth.	T81 E	Brazil nuts	Brooklyn, N.Y.	.....	.....	x
454..	C. berth.	T96 A	Brazil nuts	Storrs, Conn.	.....	.....	x
455..	C. A.	T96 E	Brazil nuts	Storrs, Conn.	.....	.....	x
456..	C. berth.	T96 C	Brazil nuts	Storrs, Conn.	x	.....	.....
457..	C. berth.	T97 B	Brazil nuts	Amsterdam, N.Y.	.....	.....	x
458..	C. berth.	T99 A	Brazil nuts	Amsterdam, N.Y.	.....	.....	x
459..	C. berth.	T99 D	Brazil nuts	Amsterdam, N.Y.	.....	.....	x
460..	C. berth.	T99 C	Brazil nuts	Amsterdam, N.Y.	.....	.....	x
461..	C. berth.	T100 A	Brazil nuts	Amsterdam, N.Y.	.....	.....	x
462..	C. berth.	T101 A	Brazil nuts	Amsterdam, N.Y.	.....	.....	x
463..	C. berth.	T101 B	Brazil nuts	Amsterdam, N.Y.	.....	.....	x
464..	C. berth.	T101 C	Brazil nuts	Amsterdam, N.Y.	x	.....	.....
465..	C. berth.	T98	Brazil nuts	Amsterdam, N.Y.	x	.....	.....
466..	C. eleg.	T29 D	Soil	Cold Spring Harbor	x	.....	.....
467..	C. eleg.	T36 B	Soil	Cold Spring Harbor	.....	x	.....
468..	C. eleg.	T36 C	Soil	Cold Spring Harbor	.....	.....	x
469..	C. eleg.	T44 D	Soil	Cold Spring Harbor	x	.....	.....
470..	C. eleg.	T58 D	Soil	Cold Spring Harbor	x	.....	.....

TABLE III—*Continued*

Race no.	Species	Culture no.	Substratum	Locality represented	Plus	Neutral	Minus
471..	C. eleg.	T60 B	Soil	Cold Spring Harbor	x	.....	.....
472..	C. eleg.	T60 D	Soil	Cold Spring Harbor	.....	.....	x
473..	C. eleg.	T60 E	Soil	Cold Spring Harbor	x	.....	.....
474..	C. eleg.	T61 D	Soil	Cold Spring Harbor	x	.....	.....
475..	C. eleg.	T61 C	Soil	Cold Spring Harbor	.....	.....	x
476..	C. eleg.	T61 E	Soil	Cold Spring Harbor	.....	.....	x
477..	C. eleg.	T61 G	Soil	Cold Spring Harbor	.....	.....	x
478..	C. eleg.	T62 A	Soil	Cold Spring Harbor	.....	.....	x
479..	C. eleg.	T62 A	Soil	Cold Spring Harbor	.....	.....	x
480..	C. eleg.	T63 A	Soil	Cold Spring Harbor	.....	.....	x
481..	C. eleg.	T64 D	Soil	Cold Spring Harbor	x	.....	.....
482..	C. eleg.	T64 C	Soil	Cold Spring Harbor	x	.....	.....
483..	C. eleg.	T64 E	Soil	Cold Spring Harbor	.....	.....	x
484..	C. eleg.	T64 F	Soil	Cold Spring Harbor	x	.....	.....
485..	C. eleg.	T65 C	Soil	Cold Spring Harbor	x	.....	.....
486..	C. eleg.	T65 A	Soil	Cold Spring Harbor	.....	.....	x
487..	C. eleg.	T84 A	Soil	Cold Spring Harbor	x	.....	.....
488..	C. eleg.	T84 B	Soil	Cold Spring Harbor	.....	.....	x
489..	C. eleg.	T84 D	Soil	Cold Spring Harbor	.....	.....	x
490..	C. eleg.	T85 B	Soil	Cold Spring Harbor	.....	.....	x
491..	C. eleg.	T85 D	Soil	Cold Spring Harbor	.....	.....	x
492..	C. eleg.	T85 E	Soil	Cold Spring Harbor	x	.....	.....
493..	C. eleg.	T86 A	Soil	Cold Spring Harbor	x	.....	.....
494..	C. eleg.	T86 C	Soil	Cold Spring Harbor	x	.....	.....
495..	C. eleg.	T86 E	Soil	Cold Spring Harbor	x	.....	.....
496..	C. eleg.	T86 F	Soil	Cold Spring Harbor	x	.....	.....
497..	C. eleg.	T86 G	Soil	Cold Spring Harbor	x	.....	.....
498..	C. eleg.	T87 B	Soil	Cold Spring Harbor	x	.....	.....
499..	C. eleg.	T87 F	Soil	Cold Spring Harbor	x	.....	.....
500..	C. eleg.	T89 A	Soil	Cold Spring Harbor	x	.....	.....
501..	C. eleg.	T89 B	Soil	Cold Spring Harbor	x	.....	.....
502..	C. eleg.	T89 C	Soil	Cold Spring Harbor	x	.....	.....
503..	C. eleg.	T92 B	Soil	Cold Spring Harbor	x	.....	.....
504..	C. eleg.	T92 D	Soil	Cold Spring Harbor	x	.....	.....
505..	C. eleg.	T92 D	Soil	Cold Spring Harbor	x	.....	.....
506..	C. eleg.	T92 E	Soil	Cold Spring Harbor	.....	.....	x
507..	C. eleg.	T92 G	Soil	Cold Spring Harbor	.....	.....	x
508..	C. A.	T52	Brazil nuts	New York City	x	.....	.....
510..	C. ech.	.....	Laboratory infection	Washington, D.C.	.....	.....	x
511..	C. A.	T73 D	Brazil nuts	New York City	.....	.....	x
512..	C. A.	T75 A	Brazil nuts	New York City	x	.....	.....
513..	C. A.	T75 B	Brazil nuts	New York City	.....	.....	x
514..	C. A.	T75 C	Brazil nuts	New York City	.....	.....	x
515..	C. A.	T75 F	Brazil nuts	New York City	x	.....	.....
516..	C. A.	T76 A	Brazil nuts	New York City	.....	.....	x
517..	C. A.	T76 D	Brazil nuts	New York City	.....	.....	x
518..	C. A.	T76 E	Brazil nuts	New York City	.....	.....	x
519..	C. A.	T79 B	Brazil nuts	New York City	.....	.....	x
520..	C. A.	T79 F	Brazil nuts	New York City	.....	.....	x
521..	C. A.	T80 A	Brazil nuts	New York City	x	.....	.....
522..	C. A.	T81 C	Brazil nuts	Brooklyn, N.Y.	x	.....	.....
523..	C. A.	T81 G	Brazil nuts	Brooklyn, N.Y.	.....	.....	x
524..	C. A.	T96 E	Brazil nuts	Storrs, Conn.	x	.....	.....

TABLE III—*Continued*

Race no.	Species	Culture no.	Substratum	Locality represented	Plus	Neutral	Minus
525..	C. ech.	T98 C	Brazil nuts	Amsterdam, N.Y.	x	.....	.....
526..	C. ech.	T99 A	Brazil nuts	Amsterdam, N.Y.	.....	.....	x
527..	C. ech.	T97 A	Brazil nuts	Amsterdam, N.Y.	x	.....	.....
528..	C. ech.	T99 E	Brazil nuts	Amsterdam, N.Y.	x	.....	.....
529..	C. ech.	T99 E	Brazil nuts	Amsterdam, N.Y.	.....	.....	x
718..	C. berth.	T111 E	Brazil nuts	Norway, Me.	.....	.....	x
719..	C. berth.	T112 F	Brazil nuts	Parkersburg, W.Va.	.....	.....	x
720..	C. berth.	T113 C	Brazil nuts	Louisville, Ky.	.....	x	.....
721..	C. berth.	T114 A	Brazil nuts	Franklin, Ind.	.....	.....	x
722..	C. berth.	T114 D	Brazil nuts	Franklin, Ind.	.....	.....	x
723..	C. berth.	T115 A	Brazil nuts	Hickory, N.C.	.....	x	.....
724..	C. berth.	T115 B	Brazil nuts	Hickory, N.C.	.....	.....	x
725..	C. berth.	T115 B	Brazil nuts	Hickory, N.C.	.....	.....	x
726..	C. berth.	T115 F	Brazil nuts	Hickory, N.C.	.....	.....	x
727..	C. berth.	T116 B	Brazil nuts	Knoxville, Tenn.	.....	.....	x
728..	C. berth.	T116 C	Brazil nuts	Knoxville, Tenn.	.....	.....	x
729..	C. berth.	T116 G	Brazil nuts	Knoxville, Tenn.	.....	.....	x
730..	C. berth.	T117 B	Brazil nuts	Knoxville, Tenn.	.....	.....	x
731..	C. berth.	T117 B	Brazil nuts	Knoxville, Tenn.	.....	.....	x
732..	C. berth.	T117 B	Brazil nuts	Knoxville, Tenn.	.....	.....	x
733..	C. berth.	T117 B	Brazil nuts	Knoxville, Tenn.	.....	.....	x
734..	C. berth.	T117 C	Brazil nuts	Knoxville, Tenn.	.....	.....	x
735..	C. berth.	T117 C	Brazil nuts	Knoxville, Tenn.	.....	.....	x
736..	C. berth.	T117 D	Brazil nuts	Knoxville, Tenn.	.....	.....	x
737..	C. berth.	T117 D	Brazil nuts	Knoxville, Tenn.	.....	.....	x
738..	C. berth.	T117 D	Brazil nuts	Knoxville, Tenn.	x	.....	.....
739..	C. berth.	T117 E	Brazil nuts	Knoxville, Tenn.	.....	.....	x
740..	C. berth.	T118 A	Brazil nuts	Knoxville, Tenn.	.....	.....	x
741..	C. berth.	T118 D	Brazil nuts	Knoxville, Tenn.	.....	.....	x
742..	C. A.	T111 A	Brazil nuts	Norway, Me.	.....	.....	x
743..	C. A.	T111 B	Brazil nuts	Norway, Me.	.....	.....	x
744..	C. A.	T111 C	Brazil nuts	Norway, Me.	.....	.....	x
745..	C. A.	T111 G	Brazil nuts	Norway, Me.	.....	x	.....
747..	C. ech.	T113 B	Brazil nuts	Louisville, Ky.	x	.....	.....
748..	C. A.	T113 B	Brazil nuts	Louisville, Ky.	x	.....	.....
749..	C. A.	T113 B	Brazil nuts	Louisville, Ky.	x	.....	.....
750..	C. ech.	T113 C	Brazil nuts	Louisville, Ky.	.....	.....	x
751..	C. A.	T113 D	Brazil nuts	Louisville, Ky.	.....	.....	x
752..	C. A.	T113 D	Brazil nuts	Louisville, Ky.	x	.....	.....
753..	C. A.	T116 A	Brazil nuts	Knoxville, Tenn.	.....	.....	x
754..	C. A.	T116 D	Brazil nuts	Knoxville, Tenn.	.....	x	.....
755..	C. A.	T116 D	Brazil nuts	Knoxville, Tenn.	x	.....	.....
756..	C. ech.	T116 E	Brazil nuts	Knoxville, Tenn.	.....	.....	x
757..	C. A.	T116 E	Brazil nuts	Knoxville, Tenn.	.....	.....	x
758..	C. A.	T116 H	Brazil nuts	Knoxville, Tenn.	.....	.....	x
759..	C. A.	T118 D	Brazil nuts	Knoxville, Tenn.	x	.....	.....
779..	C. berth.	T115 D	Brazil nuts	Hickory, N.C.	x	.....	.....
885..	C. ech.	.....	Laboratory culture	Cambridge, Mass.	x	.....	.....
886..	C. ech.	.....	Laboratory culture	Cambridge, Mass.	.....	.....	x

contrasts than to attempt to secure more accurate records by averaging the grades of a relatively few contrasts which had been several times repeated. If any of the cultures had become infected or in any other way appeared abnormal, the contrasts of course were repeated. In a few cases, especially in the earlier contrasts with *C. bertholletiae*, zygospores were found where, on the basis of a strict sexual dimorphism, they would not be expected. A repetition of these contrasts under improved technique gave the results incorporated in table VII A, and indicated that their earlier aberrant behavior was due to infection with the opposite sexes of the same species. All contrasts with species of *Cunninghamella* have been grown in the incubating oven at 24°–27°C.

Cunninghamella elegans

Table IV shows the tests with *C. elegans*. Twelve races were used as testers, and in all 426 contrast combinations were made with the total forty-two races. Of these, twenty-five were plus, sixteen were minus, and one, on account of its failure to show reactions in any of the combinations tested, has provisionally been listed as a neutral.

Cunninghamella echinulata

Table V shows the tests with *C. echinulata*. All the 153 possible contrast combinations were made with the total eighteen races. Of these, ten were plus, eight were minus, and none failed to show a sexual reaction in at least two contrast combinations. Since no reactions occurred when races with like sign were contrasted together, only the contrasts between plus and minus races are represented in the table.

Cunninghamella a

Table VI shows the tests with the undetermined species of *Cunninghamella* provisionally termed *Cunninghamella A*. It is a form intermediate in appearance between *C. bertholletiae* and *C. echinulata*, and was at first confused with them. In tube cultures it approaches more nearly the habit and color of *C. echinulata*. From this species, however, it may readily be distinguished microscopically, especially by the lack of conspicuous echinulations on the conidia. The form, however, needs a more careful study than

TABLE IV

SUMMARY OF TESTS OF *Cunninghamella elegans:* RELATIVE STRENGTH OF ZYGOSPORE FORMATION IN DIFFERENT COMBINATIONS INDICATED BY LETTERS A TO D; ABSENCE OF ZYGOSPORES INDICATED BY O; GRADES ASSIGNED TO INDIVIDUAL RACES ARE MEANS OF THEIR REACTIONS WITH TESTERS OF OPPOSITE SEX; NO. 230 NUTRIENT USED, CONSISTING OF 2 PER CENT AGAR, 2 PER CENT DRY MALT EXTRACT, 2 PER CENT DEXTROSE, AND 0.1 PER CENT MEAT PEPTONE.

Grade	Races	Minus testers					Plus testers						
		475	472	468	478	507	496	466	474	469	470	471	473
	Plus races												
2.80	496	B	B	B	B	C	....	O	O	O	O	O	O
2.60	482	A	B	B	C	D	O	O	O	O	O	O	O
2.40	487	B	A	B	D	D	O	O	O	O	O	O	O
2.40	505	C	B	B	D	B	O	O	O	O	O	O	O
2.20	466	B	C	D	C	B	O	....	O	O	O	O	O
2.20	474	A	A	C	D	O	O	O	....	O	O	O	O
2.20	494	A	B	C	D	D	O	O	O	O	O	O	O
2.20	499	B	B	B	C	O	O	O	O	O	O	O	O
2.20	504	B	B	C	D	C	O	O	O	O	O	O	O
2.00	469	C	B	C	B	O	O	O	O	....	O	O	O
2.00	500	B	C	B	D	D	O	O	O	O	O	O	O
2.00	502	C	C	C	D	B	O	O	O	O	O	O	O
1.80	471	C	B	B	D	O	O	O	O	O	O	....	O
1.80	497	C	C	C	C	D	O	O	O	O	O	O	O
1.60	470	C	C	B	D	O	O	O	O	O	....	O	O
1.60	484	B	C	D	D	D	O	O	O	O	O	O	O
1.60	498	C	C	C	C	O	O	O	O	O	O	O	O
1.40	492	D	O	B	D	C	O	O	O	O	O	O	O
1.40	473	D	D	D	C	C	O	O	O	O	O	O	....
1.40	481	C	C	C	D	O	O	O	O	O	O	O	O
1.40	485	C	C	C	D	O	O	O	O	O	O	O	O
1.40	493	C	C	D	D	D	O	O	O	O	O	O	O
1.40	495	C	C	D	D	D	O	O	O	O	O	O	O
1.40	503	C	D	D	D	C	O	O	O	O	O	O	O
1.00	501	O	O	C	C	D	O	O	O	O	O	O	O
	Neutral races												
0.00	467	O	O	O	O	O	O	O	O	O	O	O	O
	Minus races												
2.71	506	O	O	O	O	O	B	C	B	B	B	B	C
2.57	472	O	....	O	O	O	B	C	A	B	C	B	D
2.57	476	O	O	O	O	O	B	B	B	B	C	B	D
2.57	480	O	O	O	O	O	B	B	C	C	A	B	D
2.43	475	....	O	O	O	O	B	B	A	C	C	C	D
2.29	479	O	O	O	O	O	C	B	C	C	C	B	C
2.29	489	O	O	O	O	O	B	B	C	C	C	C	C
2.14	468	O	O	....	O	O	B	D	C	C	B	B	D
2.14	488	O	O	O	O	O	B	C	B	C	C	C	D
2.14	490	O	O	O	O	O	B	C	C	C	C	C	C
1.86	478	O	O	O	....	O	B	C	D	B	D	D	C
1.86	483	O	O	O	O	O	A	C	D	C	D	C	D
1.71	491	O	O	O	O	O	C	C	C	C	C	D	D
1.71	486	O	O	O	O	O	B	C	C	C	C	O	D
1.00	507	O	O	O	O	....	C	B	O	O	O	O	C
0.71	477	O	O	O	O	O	O	D	D	D	D	D	O
Grades (all combinations)		2.36	2.24	2.12	1.44	1.12	2.69	2.25	2.12	2.06	1.94	1.94	1.31

it has received before it can justly be described as a distinct species. The manner in which the races reacted in combinations first suggested that another species was included in the collections, and a later inspection and microscopic examination showed that species

TABLE V

SUMMARY OF TESTS OF *Cunninghamella echinulata:* RELATIVE STRENGTH OF ZYGOSPORE FORMATION IN DIFFERENT COMBINATIONS INDICATED BY LETTERS A TO D; ABSENCE OF ZYGOSPORES INDICATED BY O; GRADES ASSIGNED TO INDIVIDUAL RACES ARE MEANS OF THEIR REACTIONS WITH TESTERS OF OPPOSITE SEX; CONTRASTS BETWEEN RACES OF SAME SEX MADE BUT NOT REPRESENTED; IN ALL CASES THEY FAILED TO PRODUCE ZYGOSPORES; NO. 362 NUTRIENT USED, CONSISTING OF 2 PER CENT AGAR, 2 PER CENT WHEY POWDER, AND 1 PER CENT DEXTROSE.

Grade	Minus races	Grade									
		2.50	2.25	1.87	1.63	1.63	1.50	1.25	1.25	1.13	0.50
		Plus races									
		747	885	527	229	525	238	236	255	248	528
2.70	886	B	B	B	B	B	C	B	B	C	C
2.30	265	C	C	C	C	B	C	C	B	B	C
2.00	750	C	B	B	A	O	B	B	D	D	O
1.60	510	B	B	B	C	C	C	O	D	O	O
1.50	529	B	C	C	C	O	C	C	O	C	O
1.10	526	C	B	O	O	B	O	O	C	D	O
0.70	756	C	C	C	O	O	D	O	O	O	O
0.50	250	B	O	O	O	C	O	O	O	O	O

A could be distinguished from the other species. Six races were used as testers, and in all 297 contrast combinations were made with the total fifty-three races. Of these, twenty-two were plus, twenty-nine were minus, and two, on account of their failure to show reactions in any of the combinations tested, were listed as neutrals. Imperfect sexual reactions, indicated by small letters in table VI, will be discussed under the following species.

CUNNINGHAMELLA BERTHOLLETIAE

Table VII *A* shows the tests with *C. bertholletiae*. Fifteen races were used as testers, and in all 1215 combinations were made with the total eighty-nine races. Of these, twelve were plus, sixty-nine were minus, and eight, on account of their failure to show reactions

TABLE VI

SUMMARY OF TESTS OF *Cunninghamella A:* RELATIVE STRENGTH OF ZYGOSPORE FORMATIONS IN DIFFERENT COMBINATIONS INDICATED BY CAPITAL LETTERS A TO D; STRENGTH OF IMPERFECT REACTIONS BY SMALL LETTERS a TO d; ABSENCE OF SEXUAL REACTIONS INDICATED BY O; GRADES ASSIGNED TO INDIVIDUAL RACES ARE MEANS OF THEIR REACTIONS WITH TESTERS OF OPPOSITE SEX; NO. 362 NUTRIENT USED, CONSISTING OF 2 PER CENT AGAR, 2 PER CENT WHEY POWDER, AND 1 PER CENT DEXTROSE.

Grade	Races	Minus testers			Plus testers		
		269	182	257	515	242	181
	Plus races						
4.00	515	A	A	A	.....	O	O
3.67	242	A	A	B	O	.....	O
3.33	181	B	B	A	O	O	.....
3.00	191	B	B	B	O	O	O
2.67	759	C	B	B	O	O	O
2.33	267	C	C	B	O	O	O
2.33	748	C	B	C	O	O	O
2.00	261	C	C	C	O	O	O
2.00	755	C	C	C	O	O	O
1.67	235	C	C	D	O	O	O
1.67	259	C	C	D	O	O	O
1.67	508	C	D	C	O	O	O
1.67	521	D	C	C	O	O	O
1.67	749	D	C	C	O	O	O
1.33	260	C	D	D	O	O	O
1.33	273	C	D	D	O	O	O
1.33	524	D	C	D	O	O	O
1.00	190	D	D	D	O	O	O
1.00	512	D	O	C	O	O	O
0.67	522	D	D	O	O	O	O
0.33	752	D	O	O	O	O	O
0.33	193	D	O	O	O	O	O
	Neutral races						
0.00	745	O	O	O	O	O	O
0.00	754	O	O	O	O	O	O
	Minus races						
3.67	182	O	.....	O	A	A	B
3.67	257	O	O	.....	A	B	A
3.67	269	.....	O	O	A	A	B
3.33	517	O	O	O	A	b	b
3.33	523	O	O	O	A	b	b
3.00	744	O	O	O	A	C	B
3.00	455	O	O	O	A	C	B
2.33	514	O	O	O	A	D	C
2.33	256	O	O	O	B	C	C
1.67	224	O	O	O	B	D	D
1.67	188	O	O	O	d	b	D
1.33	513	O	O	O	B	O	D
1.00	239	O	O	O	B	O	O
1.00	751	O	O	O	b	O	O
0.67	184	O	O	O	C	O	O
0.67	270	O	O	O	C	O	O

TABLE VI—*Continued*

Grade	Races	Minus testers			Plus testers		
		269	182	257	515	242	181
	Minus races						
0.67	272	O	O	O	C	O	O
0.67	511	O	O	O	C	O	O
0.67	516	O	O	O	C	O	O
0.67	518	O	O	O	C	O	O
0.67	520	O	O	O	C	O	O
0.67	742	O	O	O	C	O	O
0.67	743	O	O	O	C	O	O
0.67	753	O	O	O	C	O	O
0.67	758	O	O	O	C	O	O
0.67	757	O	O	O	c	O	O
0.67	187	O	O	O	c	O	O
0.33	225	O	O	O	D	O	O
0.33	519	O	O	O	O	O	d
Grades (all combinations) .		1.91	1.86	1.82	2.59	0.97	1.03

in any of the combinations tested, have been provisionally listed as neutral.

C. bertholletiae seems to differ from the other species of *Cunninghamella* investigated except species *A*, and in fact from all the other mucors which have been studied in the same manner, in that between certain races imperfect sexual reactions have been found which do not lead to zygospore formation. It is possible that such reactions may occur more frequently than is realized. In contrasting the first few testers of a given species, the practice has been to look for imperfect reactions at an early stage of development, and, if none are found, to examine the culture dishes in later series only at the end of the growth period when imperfect reactions would not readily be recognized. It is thus possible that some of the zero records for the contrasts of species *A* in table VI would be replaced by grades of imperfect sexual reaction if they had all been retested and inspected at an early growth period. Imperfect reactions are graded in the tables by small letters instead of by the capitals used for zygospore formation. The reaction might readily be confused with the early stages of zygospore formation or the final stages of "imperfect hybridization." Imperfect hybridization has heretofore been found to occur only between the opposite sexes of different species. When dealing with races of

TABLE VII

SUMMARY OF TESTS OF *Cunninghamella bertholletiae:* RELATIVE STRENGTH OF ZYGOSPORE FORMATION IN DIFFERENT COMBINATIONS INDICATED BY CAPITAL LETTERS A TO D, RELATIVE STRENGTH IN IMPERFECT SEXUAL REACTION INDICATED BY SMALL LETTERS a TO d; PRODUCTION OF PARTHENOSPORES (*a*-ZYGOSPORES) INDICATED BY CAPITAL LETTER FOLLOWED BY AN ASTERISK; ABSENCE OF OBSERVED SEXUAL REACTION INDICATED BY O; GRADES ASSIGNED TO INDIVIDUAL RACES ARE MEANS OF THEIR SEXUAL REACTIONS WITH TESTERS OF OPPOSITE SEX; NO. 230 NUTRIENT USED, CONSISTING OF 2 PER CENT AGAR, 2 PER CENT DRY MALT EXTRACT, 2 PER CENT DEXTROSE, AND 0.1 PER CENT MEAT PEPTONE.

GRADE	RACES	*A.* INTRASPECIFIC REACTIONS															*B.* REACTIONS WITH SPECIES A				
		Minus testers							Neutral testers		Plus testers						Minus testers			Plus testers	
		266	457	459	213	183	241	180	215	452	217	227	268	234	464	456	188	455	269	191	515
	Plus races																				
3.00	217.....	A	B	B	B	b	b	C	O	O	...	O	O	O	O	O	d	c	C*	O	...
2.71	234.....	b	b	c	b	c	b	b	O	O	O	O	O	...	O	O	b	d	C*	O	O
2.71	268.....	B	A	B	B	c	c	c	O	O	O	O	...	O	O	O	c	b	C*	O	...
2.57	465.....	C	b	B	b	c	b	C	O	O	O	O	O	O	O	O	...	...	D*	O	...
2.57	227.....	B	C	B	B	c	b	c	O	O	O	...	O	O	O	O	c	...	C*	O	...
2.43	464.....	B	B	B	B	c	d	C	O	O	O	O	O	O	...	O	c	...	D*	O	...
2.14	738.....	B	C	B	A	D	O	c	O	O	O	O	O	O	O	O	...	...	...	O	...
1.71	179.....	b	c	D	d	b	C	O	O	O	O	O	O	O	O	O	...	...	C*	O	...
1.43	456.....	C	b	c	D	d	O	d	O	O	O	O	O	O	O	...	O	...	...	O	...
1.29	218.....	D	c	c	O	C	C	O	O	O	O	O	O	O	O	O	...	...	O	O	...
1.29	271.....	c	C	c	d	c	O	O	O	O	O	O	O	O	O	O	...	...	C*	O	O
0.43	779.....	D	O	D	O	O	D	O	O	O	O	O	O	O	O	O	...	...	...	O	...
	Neutral races																				
0.00	215.....	O	O	O	O	O	O	O	...	O	O	O	O	O	O	O	O	...	...	O	...
0.00	247.....	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	...	...	...	O	...
0.00	249.....	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	...	...	...	O	...
0.00	373.....	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	...	...	...	O	...
0.00	450.....	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	...	...	...	O	...
0.00	452.....	O	O	O	O	O	O	O	O	...	O	O	O	O	O	O	O	...	...	O	...
0.00	720.....	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	...	...	...	O	...
0.00	723.....	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	...	...	...	O	...
	Minus races																				
3.00	732.....	O	O	O	O	O	O	O	O	O	A	A	B	C	B	c	...	...	O	b	C*
3.00	266.....	...	O	O	O	O	O	O	O	O	A	B	B	b	B	C	O	O	...	d	...
3.00	274.....	O	O	O	O	O	O	O	O	O	B	B	B	b	A	c	...	...	O	c	...
3.00	729.....	O	O	O	O	O	O	O	O	O	A	A	A	O	A	c	...	...	O	c	...
3.00	457.....	O	...	O	O	O	O	O	O	O	B	C	A	b	B	b	O	O	...	c	...
2.83	737.....	O	O	O	O	O	O	O	O	O	A	B	B	c	B	c	...	...	...	c	...
2.67	213.....	O	O	O	...	O	O	O	O	O	B	B	B	b	B	D	O	...	O	c	...
2.67	252.....	O	O	O	O	O	O	O	O	O	B	B	B	c	B	c	...	...	...	b	...
2.67	262.....	O	O	O	O	O	O	O	O	O	A	B	B	b	B	O	...	...	...	O	...
2.67	459.....	O	O	...	O	O	O	O	O	O	B	B	B	c	B	c	O	...	O	c	...
2.50	731.....	O	O	O	O	O	O	O	O	O	B	B	B	C	B	d	...	...	...	a	D*
2.50	736.....	O	O	O	O	O	O	O	O	O	A	A	B	O	C	c	...	...	...	b	...
2.33	458.....	O	O	O	O	O	O	O	O	O	C	C	C	b	B	c	...	...	...	b	...
2.17	219.....	O	O	O	O	O	O	O	O	O	B	D	C	a	B	O	...	...	...	D	...
2.00	180.....	O	O	O	O	O	O	...	O	O	C	c	c	b	C	d	O	...	O	O	...
2.00	183.....	O	O	O	O	...	O	O	O	O	b	c	c	c	c	d	O	O	O	b	...

TABLE VII—*Continued*

GRADE	RACES	A. INTRASPECIFIC REACTIONS															B. REACTIONS WITH SPECIES A				
		Minus testers							Neutral testers		Plus testers						Minus testers			Plus testers	
		266	457	459	213	183	241	180	215	452	217	227	268	234	464	456	188	455	269	191	515
	Minus races																				
2.00	241	O	O	O	O	O	...	O	O	O	b	b	c	b	d	O	O	O	O	c	...
1.67	186	O	O	O	O	O	O	O	O	O	b	c	c	b	O	O	...	...	...	O	...
1.67	244	O	O	O	O	O	O	O	O	O	b	b	c	c	O	O	...	...	...	b	...
1.50	192	O	O	O	O	O	O	O	O	O	d	c	c	c	c	O	...	...	...	O	...
1.50	216	O	O	O	O	O	O	O	O	O	b	c	c	c	O	O	...	...	...	O	...
1.50	223	O	O	O	O	O	O	O	O	O	b	c	c	c	O	O	...	...	...	c	...
1.50	226	O	O	O	O	O	O	O	O	O	c	c	c	c	d	O	...	...	...	O	...
1.50	232	O	O	O	O	O	O	O	O	O	c	c	c	O	B	O	...	...	...	c	...
1.50	233	O	O	O	O	O	O	O	O	O	b	c	c	c	O	O	...	...	...	O	...
1.50	451	O	O	O	O	O	O	O	O	O	b	c	c	O	O	c	...	...	...	O	...
1.33	221	O	O	O	O	O	O	O	O	O	c	c	c	c	O	O	...	...	...	d	...
1.33	258	O	O	O	O	O	O	O	O	O	C	c	c	d	D	O	...	...	...	O	...
1.33	448	O	O	O	O	O	O	O	O	O	d	c	c	d	O	c	...	...	...	b	...
1.33	463	O	O	O	O	O	O	O	O	O	b	c	c	d	O	O	...	...	...	O	...
1.33	733	O	O	O	O	O	O	O	O	O	c	O	d	d	c	c	...	...	...	b	...
1.17	185	O	O	O	O	O	O	O	O	O	D	c	c	d	d	O	...	...	...	b	...
1.17	189	O	O	O	O	O	O	O	O	O	d	c	c	c	O	O	...	...	...	O	...
1.17	222	O	O	O	O	O	O	O	O	O	d	c	c	c	O	O	...	...	...	c	...
1.17	243	O	O	O	O	O	O	O	O	O	c	c	c	d	O	O	...	...	...	O	...
1.17	275	O	O	O	O	O	O	O	O	O	c	c	c	d	O	O	...	...	...	b	...
1.17	460	O	O	O	O	O	O	O	O	O	B	c	c	O	O	O	...	...	...	c	...
1.17	461	O	O	O	O	O	O	O	O	O	c	c	c	d	O	O	...	...	...	O	...
1.17	718	O	O	O	O	O	O	O	O	O	B	d	O	O	C	d	...	...	...	O	...
1.00	220	O	O	O	O	O	O	O	O	O	c	c	c	O	O	O	...	...	...	O	...
1.00	228	O	O	O	O	O	O	O	O	O	c	c	c	O	O	O	...	...	...	O	...
1.00	254	O	O	O	O	O	O	O	O	O	c	c	c	O	O	O	...	...	...	O	...
1.00	446	O	O	O	O	O	O	O	O	O	d	c	c	d	O	O	...	...	...	a	...
1.00	449	O	O	O	O	O	O	O	O	O	d	c	c	d	O	O	...	...	...	c	...
0.83	214	O	O	O	O	O	O	O	O	O	d	c	c	O	O	O	...	...	...	c	...
0.83	240	O	O	O	O	O	O	O	O	O	d	c	c	O	O	O	...	...	...	c	...
0.83	246	O	O	O	O	O	O	O	O	O	d	c	c	O	O	O	...	...	...	O	...
0.83	447	O	O	O	O	O	O	O	O	O	d	c	c	O	O	O	...	...	...	c	...
0.83	453	O	O	O	O	O	O	O	O	O	d	c	c	O	O	O	...	...	...	c	...
0.83	454	O	O	O	O	O	O	O	O	O	d	c	c	O	O	O	...	...	...	O	...
0.83	462	O	O	O	O	O	O	O	O	O	d	c	c	O	O	O	...	...	...	O	...
0.83	741	O	O	O	O	O	O	O	O	O	c	d	O	O	O	C	...	...	...	d	...
0.83	372	O	O	O	O	O	O	O	O	O	d	O	O	a	O	O	...	...	...	O	...
0.67	253	O	O	O	O	O	O	O	O	O	c	c	O	O	O	O	...	...	...	b	...
0.67	722	O	O	O	O	O	O	O	O	O	d	O	O	O	b	O	...	...	...	c	...
0.67	726	O	O	O	O	O	O	O	O	O	c	O	O	O	c	O	...	...	...	c	...
0.67	730	O	O	O	O	O	O	O	O	O	c	O	d	O	d	O	...	...	...	O	...
0.67	735	O	O	O	O	O	O	O	O	O	B	O	O	O	d	O	...	...	...	d	...
0.67	740	O	O	O	O	O	O	O	O	O	c	O	O	O	c	O	...	...	...	c	...
0.50	721	O	O	O	O	O	O	O	O	O	d	O	O	O	O	C	...	...	...	c	...
0.50	734	O	O	O	O	O	O	O	O	O	c	O	O	O	d	O	...	...	...	c	...
0.33	237	O	O	O	O	O	O	O	O	O	O	O	c	O	O	O	...	...	...	O	...
0.33	245	O	O	O	O	O	O	O	O	O	d	d	O	O	O	O	...	...	...	O	...

TABLE VII—*Continued*

Grade	Races	A. Intraspecific reactions																B. Reactions with species A				
		Minus testers							Neutral testers		Plus testers							Minus testers			Plus testers	
		266	457	459	213	183	241	180	215	450	217	227	268	234	464	456	188	455	269	191	515
	Minus races																				
0.33	719.....	O	O	O	O	O	O	O	O	O	c	O	O	O	O	O	...	...	...	c	...
0.33	724.....	O	O	O	O	O	O	O	O	O	d	O	O	O	d	O	...	...	...	c	...
0.33	727.....	O	O	O	O	O	O	O	O	O	c	O	O	O	O	O	...	...	...	c	...
0.33	728.....	O	O	O	O	O	O	O	O	O	d	O	O	O	d	O	...	...	...	a	...
0.33	739.....	O	O	O	O	O	O	O	O	O	O	O	O	O	c	O	...	...	...	O	...
0.17	725.....	O	O	O	O	O	O	O	O	O	d	O	O	O	O	O	...	...	...	c	...
Grades (all combinations).....		2.50	2.42	2.33	2.08	1.83	1.67	1.33	0.00	0.00	2.09	1.71	1.68	1.09	1.07	0.52					

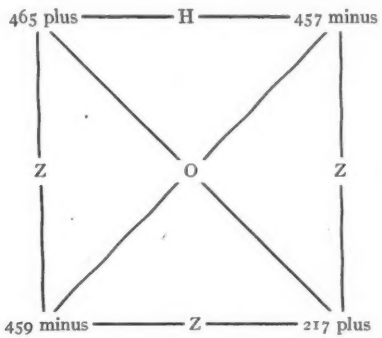
the same species, if any reaction was initiated at all, it was carried through to the production of zygospores, except of course for some obviously detrimental check in environmental conditions. The sexual process resulting in the production of zygospores may be considered the sum of two distinct reactions; first, the formation of opposed progametes or at most gametes; second, the dissolution of the cross walls between the gametes and the growth of the fusion cell into a zygospore. Only the first reaction can take place when the plus and minus races contrasted belong to different species.[5]

A number of facts indicate, however, that in the races listed under *C. bertholletiae* we are dealing with a single species. The essential uniformity of the strains in morphological appearance speaks for specific identity, and the production of zygospores fails to separate them into any consistent groups. A quadrangular reaction within selected groups of four may be discerned from table VII *A*. Thus the same four races shown in fig. 1 form the following quadrangle, in which *Z* stands for zygospore formation, *H* for imperfect sexual reaction, and *O* for no sexual reaction. Other similar quadrangles may be assembled from table VII *A*. The fact that only imperfect reactions are found in certain contrasts when

[5] True hybrids have been reported between closely related species of *Mucor* by Saito and Naganishi (19).

zygospores would be expected does not alter the sex of the races involved. When they take part in any sexual reactions at all, they are consistently either plus or minus. The first reaction of the sexual process is sufficient to indicate their sex, and gives an index of their sexual vigor. In calculating the mean grades of sexual activity for the different races, therefore, it has been considered fairest to give the imperfect reactions equal weight with zygospore formation.

What are the causes which prevent one combination in a quadrangular reaction from carrying the sexual process through to completion is a question requiring further study. In certain cases,



at least, the distance between the inoculations of opposing strains seems to be a matter of some importance. In *Circinella spinosa* it has always been necessary to inoculate the opposite sexes very close together in order to obtain zygospores, which are not formed beyond a few millimeters from the points of inoculation. In a few cases a retest of an imperfect reaction between races of *C. bertholletiae*, but with inoculations close together, has shown zygospore formation.

Certain contrasts which were repeated with inoculations at the usual distance apart gave different reactions from those first obtained, as may be seen by a comparison of table VII *A* with table VIII where the retest contrasts are listed. In table VIII there is, as might be expected, a certain amount of change in the grades assigned to the strength of the reactions. The present

interest, whoever, centers upon the grades inclosed in parentheses, which indicate reactions which have changed from a perfect to an imperfect reaction as shown by the production of stages resembling imperfect hybrids in place of zygospores. It will be seen that there are certain unexplained irregularities in the production of zygospores or of only imperfect reactions which indicate that the preliminary tests have not discovered all the factors involved. Enough has been learned, it is believed, to indicate that some of the factors are environmental which determine whether a sexual process in this species goes through to

TABLE VIII

RETESTS OF CONTRASTS BETWEEN RACES OF *Cunninghamella bertholletiae:* CAPITAL LETTERS INDICATE GRADES OF ZYGOSPORE FORMATION; SMALL LETTERS INDICATE GRADES OF IMPERFECT SEXUAL REACTION; LETTERS INCLOSED IN PARENTHESES SHOW CHANGE IN TYPE OF REACTION FROM ZYGOSPORE FORMATION TO IMPERFECT REACTIONS; REACTIONS WITH ASTERISK INDICATE PRESENCE OF PARTHENOSPORES; NO. 230 NUTRIENT USED.

Races	266	729	732	457	737	213	459	731	219	180	241	232	460	718	741	721
217			A					A		C		c	(O)	C		
234			(b)		c			(a)		c						
268										c			c			
465	C			b		b	B									
227									B							
179	c						C				(d)*					
456	C	c		c		C									(c)*	(c)*
218											C					
271	c			(c)												

completion with the formation of zygospores or is confined to the first reaction with the formation of progametes or at the most gametes.

Although environmental differences not readily controlled in the cultures may have some influence upon the extent of the sexual reaction, the genetic constitution of the individual races in the main must be responsible for their sexual behavior. We have not succeeded, however, in an attempt to subject the genetic differences to a factorial interpretation. Distinct classes of plus and minus races differing sharply in the strength of their sexual activity or in their capacity to form zygospores or only imperfect reactions with certain other races do not seem to exist. Thus certain contrasts from table VII *A* may be arranged in such a way that no

fewer than five differences in reaction are shown both in the plus and minus strains chosen to form table IX. A graded series is indicated which might indefinitely be expanded as more and more races were tested.

"Imperfect hybridization" between species

Tables IV to VII *A* deal with sexual reactions between races within the individual species concerned. In tables II, VII *B*, X, and XI are given the results of contrasting individual races of one species with those of another species. Many of the contrasts were made before the species *Cunninghamella A* was separated from

TABLE IX

Arrangement of selected races from table VII *A* showing graded differences in strength of reaction when contrasted: capital letters indicate grades of zygospores, small letters grades of imperfect sexual reaction.

Minus races	Plus races				
	217	227	456	779	234
266	A	B	C	D	b
459	B	B	c	D	c
213	B	B	D	O	b
457	B	C	b	O	b
180	C	c	d	O	b

C. echinulata and *C. bertholletiae*. Those between the testers *H* and *D* and the races of *Cunninghamella A* were made merely for the purpose of identifying the sex of the latter, and were not graded, since they were not originally intended for publication. It has seemed best, however, to include these and the reactions in table VII *B*, since they furnish cumulative evidence in regard to sexual dimorphism in *Cunninghamella*. Two races of *C. elegans* (nos. 496 and 506, respectively plus and minus) failed to show reactions with the old plus and minus testers of *C. echinulata* (nos. 885 and 886). In table VII *B* certain combinations are starred because in them the imperfect hybridization reactions led to the production of parthenospores (*a*-zygospores). When certain races of high sexual vigor are contrasted, gametes which have been formed but which have been unable to unite may develop into thick-walled sculptured

spores, which are with difficulty distinguished from the true zygospores. Superficial inspection under low magnifications would undoubtedly lead to their classification as zygospores, but it is not unlikely that in our records, especially the earlier ones on *C. bertholletiae*, contrasts may have been listed as weak zygospore reactions,

TABLE X

SUMMARY OF REACTIONS BETWEEN DIFFERENT SPECIES OF *Cunninghamella:* Z INDICATES ZYGOSPORES; SMALL LETTERS INDICATE GRADED IMPERFECT REACTIONS

	C. bertholletiae		C. echinulata		C. elegans	
	217 plus	266 minus	885 plus	886 minus	496 plus	506 minus
C. bertholletiae						
217 plus	.....	Z	O	c	O	c
266 minus	Z	.....	c	O	c	O
C. echinulata						
885 plus	O	c	.....	Z	O	O
886 minus	c	O	Z	.....	O	O
C. elegans						
496 plus	O	c	O	O	.....	Z
506 minus	c	O	O	O	Z	.....

TABLE XI

Cunninghamella A: UNGRADED "IMPERFECT HYBRIDIZATION" REACTIONS WITH PLUS AND MINUS MUCOR TESTERS *H* AND *D; H* IN BODY OF TABLE INDICATES IMPERFECT REACTIONS

Mucor	Plus races						Minus races						
	515	242	759	260	273	522	182	269	188	751	270	511	225
H plus	O	O	O	O	O	O	H	H	H	H	H	H	H
D minus	H	H	H	H	H	H	O	O	O	O	O	O	O

when they should have been called imperfect reactions with formation of parthenospores. A close examination, especially in the younger stages, will show that parthenospores develop from single gametes, and that the suspensor on only one side has a typical appearance, with what appears to be the suspensor on the opposite side frequently more or less rounded off and not closely adnate to the spore. The parthenospores themselves are often distinctly misshapen, but when the zygospores are small, as is true of those of species of *Cunninghamella*, it may be difficult to distinguish them

even with careful inspection. Parthenospores have been obtained between certain strong races of different species in other genera with larger zygospores when no doubt of their true nature was likely to occur after a careful examination. Figures of parthenospores formed on homothallic species, at stimulus of contact with a sexually vigorous race of a heterothallic species, are given in an earlier publication (**9**, *pl. 1*). The possible presence of parthenospores must not be overlooked in judging reports (**19**) of true hybridization between different species in the mucors.

So far as the reactions between different species of *Cunninghamella* have been tested, they argue for the sexual dimorphism of this genus.

Discussion

The data in the present paper refer only to the mucor genus *Cunninghamella*. A preliminary summary has already been given of tests with other genera (**10**), and it is hoped to publish a detailed account of these tests at a later date. The data so far accumulated show no behavior inconsistent with the idea of a strict sexual dimorphism. The work, especially with *Cunninghamella*, indicates that sex intergrades must be extremely rare if ever present in these forms, despite the fact that they would be expected on a priori grounds and the fact that other observers have thought they had found them.

In the species of *Cunninghamella* there is apparent a graded series so far as the strength of sexual activity is concerned, ranging from a reaction with grade *A* between sexually strong races to grade *O* between sexually weak races. Races which have shown no reactions in any contrast tested are provisionally listed as "neutral." The term neutral is obviously relative, and not meant to indicate absolute absence of sex. The number of races listed as neutral for a given collection tends to decrease as more testers are used in contrasts. Thus it is evident from table VII *A* that if strain no. 217 had not been used as a tester, strains nos. 719, 727, and 725 would have been listed as neutrals rather than as minus strains, since they would have shown no reaction against any of the plus or minus testers used. Neutrals seem to form the low

extreme of a continuously graded series of sexual vigor, and the term as applied undoubtedly includes both plus and minus races.

It is doubtful whether much significance can be attributed to the proportion of plus and minus races in the collections of the different species of *Cunninghamella* as indicative of their relative distribution in nature. In *C. bertholletiae* the minus sex seems to greatly predominate over the plus. In *C. elegans* the condition is reversed. The first species was obtained from Brazil nuts bought in different stores, mostly in or around New York City. Many of the gross cultures, therefore, may have originated from the same wholesale shipments. The races may be representative of the shipments from which they came rather than of the locality where they were grown. Experience with *Rhizopus* (4) indicates that in a mixed culture which is producing zygospores in abundance, one is likely to isolate almost exclusively one or the other of the two sexes. The cargo carriers from which the nuts originated may have been infected chiefly with minus strains. That there is considerable diversity in sexual vigor of these strains, however, is seen from the tables. *C. elegans* was obtained from different types of soil around Cold Spring Harbor, and it is possible that collections from other regions would show a predominance of the opposite sex.

The clearest result from the study of *Cunninghamella* is the fact that in 2091 contrasts (2250 including contrasts between different species of *Cunninghamella*) made between 202 races from four different species (see footnote 4) there were none which, if they showed any sexual response at all, reacted otherwise than as either a plus or a minus.

Miss ALICE M. PRICKET, Miss MARGARET CONOVER, and Miss MARY E. DRUMMOND have assisted in the progress of the investigation which is here reported.

Summary

1. The terms heterothallic and homothallic are distinguished as applied to gametophytic sexual differentiation in the mucors.

2. Types of the evidence in support of sex intergrades in heterothallic mucors are given and criticized.

3. BURGER's paper on *Cunninghamella*, in which he concludes that sexual dimorphism does not exist in this genus, is discussed (1) from the standpoint of his own data, (2) from the standpoint of our experience, and the decision is reached that his conclusion is not warranted.

4. Data on *Cunninghamella elegans*, *Cunninghamella A* (an undetermined species), *C. echinulata*, and *C. bertholletiae* give a total of 2250 contrasts between a total of 202 races.

5. In *C. bertholletiae* certain contrast combinations lead to imperfect sexual reactions when zygospores might be expected.

6. In none of the species were races found which reacted as sex intergrades.

7. It is concluded that so far as the material investigated is concerned *Cunninghamella* is sexually dimorphic.

STATION FOR EXPERIMENTAL EVOLUTION
COLD SPRING HARBOR, N.Y.

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NOTES ON WILLOWS OF SECTIONS PENTANDRAE AND NIGRAE

CARLETON R. BALL

(WITH FOUR FIGURES)

In 1905 the writer began a series of contributions under the title, *Notes on North American Willows*, of which three were published.[1] This general title has been dropped because of the great disadvantage of not being able to indicate clearly, in the title, the content and scope of each paper. For this reason the most recent contribution appeared under a specific title,[2] as does the present one. These data have been derived from studies incident to the treatment of the genus *Salix* in various floras and manuals of botany.[3]

The location of the herbarium specimens cited is as follows: B, herbarium C. R. BALL; C, Canadian Geological Survey, Ottawa; D, herbarium C. C. DEAM, Indiana; F, Field Museum, Chicago; FBb, Bebb Herbarium in Field Museum; I, Iowa State Agricultural College; N, United States National Herbarium; N.D., North Dakota Agricultural College; N.M., New Mexico Agricultural College; R, Rocky Mountain Herbarium, University of Wyoming.

SALIX SERISSIMA (Bailey) Fernald.—*S. arguta** *S. pallescens* Anderss. Svensk Vetensk. Acad. Handl. **6**:32. 1867.—*S. lucida serissima* Bailey in ARTHUR, Bull. Geol. Nat. Hist. Survey Minn.

[1] BOT. GAZ. **40**:376–380. *pls. 12, 13.* 1905; **60**:45–54. *figs. 3.* 1905; and **60**: 391–399. 1915.

[2] BALL, C. R., Undescribed willows of the section Cordatae. BOT. GAZ. **71**: 426–434. *fig. 1.* 1921.

[3] BALL, C. R., *Salix* in COULTER and NELSON, Man. Bot. Rocky Mt. Region, pp. 128–139. 1909.

———, *Salix* in PIPER and BEATTIE, Flora of the Northwest Coast, pp. 113–118. 1915.

———, *Salix* in P. C. STANDLEY, Flora of Glacier National Park, Contrib. U.S. Nat. Herb. **22**:319–324. 1921.

———, *Salix* in CHAS. C. DEAM, Trees of Indiana, revised ed., pp. 34–45. *pls. 10–14.* 1921.

3:19. 1887.—*S. serissima* (Bailey) Fernald, Rhodora 6:7. December 28, 1903.

When this species was established by FERNALD, in the very interesting and comprehensive article cited, he fully set forth its ecological characters and catalogued all available herbarium specimens. These showed its range to extend westward from Connecticut to northern Ohio, Wisconsin, and northern Minnesota. The type locality in Minnesota, and the most westerly station then known, was Mud River, Vermillion Lake, Saint Louis County, lying in the extreme northeastern part of the state, about 75 miles north of Duluth. ROBINSON and FERNALD[4] extended the range to Alberta, while the writer[5] has reported the species from Teton County, Montana. SCHNEIDER extends its range eastward to Newfoundland, north to the eastern shore of James Bay and the Severn River in Keewatin, and west to Edmonton, Banff, and Crow's Nest Lake in Alberta. The specimens cited later extend the range southwestward to Pembina and Rolette counties in North Dakota, and to Flathead County in extreme northwestern Montana. Both the Montana specimens come from the east side of the Continental Divide. Teton County lies on the plains at the eastern base of the Rocky Mountains, at an average elevation of about 4000 ft. Choteau is on the Teton River, which arises in the high mountains, but here flows eastward through the plains to the Missouri River. The localities in North Dakota are a southward extension of the distribution in Manitoba, while those in Montana obviously represent a similar extension of its distribution in the mountains of Alberta. It is quite possible that further search will extend the range both north and south in the Rocky Mountains. The Kennicott specimen from Slave River extends the range far to the north of Edmonton, into Athabasca or Mackenzie.

MONTANA.—Choteau County, Choteau, on Teton River, about 4000 ft. elevation, lat. 112°10′ W., *Griffiths* and *Lange*, August 22, 1900 (B); Flathead County, 3–4 ft. high in open marsh along Swiftcurrent Creek below Lake McDermott, alt. about 1350 m., *P. C. Standley* 16053, July 20, 1919 (B, N).

[4] ROBINSON and FERNALD, in GRAY, New Man. Bot. 322. 1908.

[5] BALL, C. R., in COULTER and NELSON, New Man. Rocky Mt. Bot. 130. 1909.

ALBERTA.—Crow Nest Lake, Rocky Mountains, *J. Macoun* 39 (Geological Survey Canada 94,440), August 8, 1897 (B); Rocky Mountains Park, Banff, low ground near the village, alt. 4500 ft., *W. C. McCalla* 2252, shrub 6 ft. tall, June 19, 1899 (N); vicinity of Banff, *N. B. Sanson* 304, July 14; 307, 309, 315A, 2167, July 15; 2173, June 27, 1911 (B); Calgary, *J. Macoun* 16 (Geological Survey Canada 94, 336), June 5, 1897 (B); Grattan Creek, near Battle River, *Macoun* and *Herriot* (Geological Survey Canada 70,252), August 17, 1906 (B).

ATHABASCA or MACKENZIE.—Slave River, *R. Kennicott*, July 1860 (N).

MANITOBA.—Bog north of Carberry, *Macoun* and *Herriot* (Geological Survey Canada 70,262), June 11, 1906 (B); near Sidney, *Macoun* and *Herriot* (Geological Survey Canada 70,263), June 12, 1906 (B) (70,264), June 13, 1906 (B).

NORTH DAKOTA.—Rolette County, Turtle Mountains, woods around Upsilon Lake (Fish Lake), *D. C. Mabbott* 464, September 7, 1917 (B); Pembina County, Walhalla, *L. R. Waldron* 1666, August 16, 1902 (B, ND).

ANDERSON in 1867 published *S. arguta* S. pallescens hirtisquama*, based on a specimen collected by BOURGEAU at Lake Winnipeg and having short aments on short peduncles, scales densely white pilose except at tips, and narrow, sharply serrate leaves. Throughout its range *S. serissima* has short aments and pilose scales, but not narrow and sharply serrate leaves. The three Manitoba specimens cited do have such leaves, and it is quite possible that they represent this form. The leaves are not quite fully developed, and it seems hardly desirable to designate them as belonging to it without more and older material. On no. 70264 the under surfaces of the leaves show scarcely any traces of glaucescence. The leaves of all three are discolored in drying, however, which tends to obscure this character.

On flowering specimens from Manitoba (*Macoun* and *Herriot* 70262) and Alberta (*Sanson* 304, 309, 2167), a peculiar appearance has been observed. The capsules, nearly or quite full sized, but not mature, are minutely roughened or papillate, and the surface, viewed by reflected light, has a striking and deceptive resemblance to a fine lustrous puberulence.

SALIX LASIANDRA Bentham.—*S. lasiandra* Benth., Pl. Hartweg, 335. 1857.—*S.-speciosa* Nutt., N. A. Sylva. **1**: 58. *pl. 17*. 1843. not HOST, 1828, or HOOKER and ARNOTT, 1832.—*S. arguta lasiandra* Anderss. Svensk. Vetensk. Akad. Handl **6**: 33. 1867 (Monog. Sal.).

—*S. lasiandra Lyallii* Sargent, Gard. and For. **8**:463. 1895.—*S. Lyallii* (Sarg.) Heller, Bull. Torr. Bot. Club **25**:580. 1898.

This beautiful species was described by BENTHAM from a staminate specimen, no. 1954, collected by HARTWEG on the Sacramento River in California. The cotype in the Gray Herbarium is a twig about 12 in. long, not fully in anthesis. The expanding leaves are only 2–4 cm. long and 5–9 mm. wide. The aments are 4 cm. long by 5–9 mm. wide.

The species had previously (1843) been described by NUTTALL from specimens observed abundantly on the Oregon and Wahlamet (Columbia and Willamette) rivers, and occasionally as far east as the Blue Mountains and the Boiseé (Snake) River.

It is a curious coincidence that FENDLER'S no. 816, collected near Santa Fe, New Mexico, and made by ANDERSSON the type of his *S. Fendleriana*, also is a staminate specimen with the aments not yet fully in anthesis and the leaves just unfolding. SCHNEIDER regards this specimen also as representing the true *S. lasiandra* rather than the green-leaved *S. caudata*, because, as he states, in some of the cotype specimens he has examined the leaves are more fully developed and show the glaucous under surface. Two specimens of this number in the National Herbarium are not sufficiently developed to show this.

The range of this species has been discussed recently by SCHNEIDER (Jour. Arnold Arb. **1**:17. 1919). Its distribution in Colorado and New Mexico, the southeasternmost extension of its range, is so restricted, and in a way so separated from the remainder, that the specimens known from these two states are listed below, in order to stimulate the interest of botanists.

COLORADO.—Montrose County, Cimarron, Gunnison River, alt. 6900 ft., *C. F. Baker* 141, June 15, 1901 (N); San Miguel County, Norwood Hill, river banks, alt. 7000 ft., *E. P. Walker* 453, August 11, 1912 (N); Archuleta County, Piedra (creek), *E. O. Wooton* 2718, August 12, 1904 (N, NM).

NEW MEXICO.—Rio Arribo County, Nutritas Creek below Tierra Amarilla, alt. 2250 m., *W. W. Eggleston* 6636, April 18–May 25, 1911 (N); meadows, vicinity of Chama, alt. 2380–2550 m., *P. C. Standley* 6645, July 9, 1911 (N); Sante Fe County, Sante Fe Canyon, 9 miles east of Sante Fe, alt. 8000 ft., *A. A.* and *E. G. Heller* 3637, June 2, 1897 (N); Sante Fe Creek, 4 miles east of Sante Fe, alt. 7500 ft., *A. A.* and *E. G. Heller* 3719, June 27,

1897 (N); McKinley County, north of Ramah, *E. O. Wooton*, July 25, 1906 (NM); Socorro County, Mogollon Mountains, middle fork of Gila River, alt. about 7000 ft., *E. O. Wooton*, August 4, 1900 (N); west fork of Gila River, alt. 6800 ft., *Wooton*, August 6, 1900 (N, NM); northwest of Mogollon Mountains, Lower Plaza, Frisco, alt. 5800 ft., *Wooton*, July 25, 1900 (N, NM); Frisco River, near Frisco, alt. 5800 ft., *Wooton*, July 25, 1900 (N).

SALIX LASIANDRA **Abramsi,** n. var.—Leaves narrowly lanceolate, 5–11 cm. long, 1–17 cm. wide, common sizes 6–7×1, 7–8×1–1.5, and 9–11×1.5 cm., margins shallowly serrulate to subentire; petioles short, 4–8–10 mm. long, thinly pubescent to glabrous, the glands of the distal upper surface small and inconspicuous or wanting; aments short, usually 2–3, sometimes 4 cm. long; capsules 5.5–7 mm. long; pedicels 1–1.5 mm. long.

This variety is named for Professor LEROY ABRAMS, of the Department of Botany of Stanford University, California, well known for his contributions to Pacific Coast botany and collector of the type specimen, his no. 4493, "near Sentinel Hotel, Yosemite Valley, Yosemite National Park, alt. 4000–4500 ft.," on June 23, 1911. It differs from the species chiefly in the smaller and narrower, less serrulate leaves, and the nearly eglandular petioles. It seems to be limited in its distribution to the Sierra Nevada of central eastern California, from Plumas County, south to Fresno County. Nearly all the specimens collected by DUDLEY in Nevada and El Dorado counties are immature and not identifiable with absolute certainty.

CALIFORNIA.—Sierra County, vicinity of Gold Lake, 1940 m., *W. W. Eggleston* 6263, 6265, August 28, 29, 1910 (N); Nevada County, lower end of Donner Lake, *A. A. Heller* 6879, July 8 (N, St.) 6943, July 16, 1903 (N, St.); vicinity of Donner Lake, *W. R. Dudley* 5007, 5008, June 12; 5018, 5026, 5027, 5049, June 14; Soda Springs station, *Dudley* 5138, June 15; flat land of the Yuba River opposite Cascade, *Dudley* 5149, 5150, June 15; by Truckee River, 1.5 miles below Truckee, *Dudley* 5155, June 17; Independence Lake, by outlet bridge, *Dudley* 5276, 5277, June 19 (all St.); Placer County, Monte Vista, Dutch Flat, *W. R. Dudley* (fol.), August 1909; El Dorado County, Glen Alpine Springs, *W. R. Dudley* 5660, June 1900 (St.); between Glen Alpine Spring and Camp Agazziz, *Dudley* 5664, June 27 (St.); Tallac House, Lake Tahoe shore, *Dudley* 5725, June 28, 1900 (St.); Glen Alpine, 6800 ft., *E. A. McGregor* 204, August 26, 1909 (St); Mariposa County, Mirror Lake, *W. R. Dudley*, June 12, 1894 (St), Yosemite National Park; near Sentinel Hotel, alt. 4000–4500 ft., *L. R. Abrams* 4493 (fem. type), June 23, 1911 (St); Merced Canyon, near Cascade Creek, 3500 ft., *Abrams* 4684, July 12, 1911 (St); Fresno County region of Sidney Creek, 5300 ft., *Hall* and *Chandler* 360, June 25–July 15 1900 (St).

SALIX CAUDATA **parvifolia,** n. var.—In the northern part of the range of *S. caudata* is found a form of lower stature and with

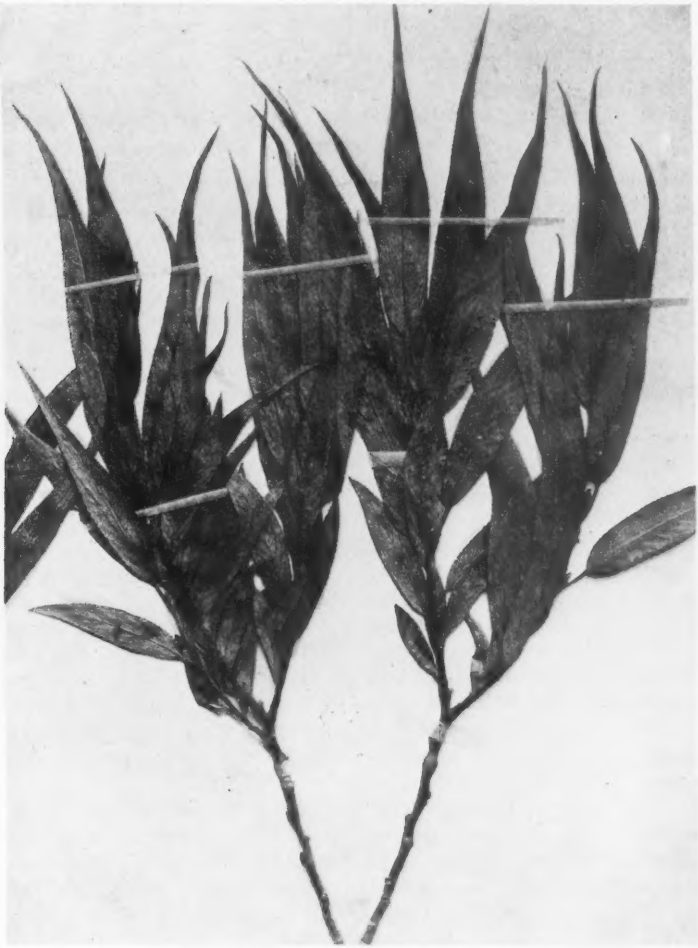

FIG. 1.—Portion of type specimen of *Salix caudata parvifolia* n. var. (nat. size)

shorter, narrower leaves (fig. 1). It occurs rather commonly and appears to be the dominant form in the mountains of northwestern

Montana and southern Alberta. While examination of a large number of specimens indicates that it passes gradually into the more typical form of the species, as do many other varieties, its recognition as a variety should help to a better understanding of the range of expression in *S. caudata*. Little is known of its height other than the notes given by STANDLEY, which indicate a lower stature than that of the species. The branchlets frequently are shorter and more divaricate; the leaves are very small, 5–8 cm. long, 7–12 mm. wide, seldom exceeding 1 cm. in width, common sizes being 6 cm.×8 mm., 7 cm.×9–10 mm., or on sterile shoots 8–10 cm.×11–16 mm., strongly glandular-serrulate, as are the stipules also. The aments are 2–3 or 3.5 cm. long, rather lax; the scales 3–3.5 mm. long, linear-lanceolate, acute to truncate or toothed, and glabrate. The capsules are 6.5–8 mm. long.

The range of variety *parvifolia* is in the Rocky Mountains from Banff, Alberta, to the Yellowstone Park in Wyoming and the Wahsatch Mountains near Ogden, Utah, also in the mountains of western Idaho and eastern Oregon, and westward in Oregon to the eastern slope of the Cascades in Wasco County.

ALBERTA.—Rocky Mountains Park, *N. B. Sanson* 164 m., June 17, 1911 (B); 265, July 5, 1911 (B); 413, 414, August 21, 1911 (B); 2056, June 22, 1912 (B).

MONTANA.—Flathead County, Glacier National Park, 6–8 ft. high, boggy meadow, along Swiftcurrent Creek, below Lake McDermott, alt. about 1350 m., *P. C. Standley* 16865 (type) August 1, 1919 (N); thicket along lake, abundant, very slender, 6–12 ft. high, vicinity of Glacier Hotel ("Lewis's"), at head of Lake McDonald, alt. 900–1050 m., *Standley* 17906, August 22, 1919 (N); Deer Lodge or Powell counties, Deer Lodge Valley, mountain streams, 5000 ft. elevation, *J. W. Blankinship* 788, m. f., May 27, 1906 (N).

WYOMING.—Yellowstone National Park, Upper Fire Hole Basin, Yellowstone Lake, *J. M. Coulter*, Hayden Survey, July 1872 (N 253728, fr.); along Lamar Creek, *J. N. Rose* 406, fr., August 20, 1893 (N).

IDAHO.—Fremont County, along an irrigating ditch, St. Anthony, *Merrill* and *Wilcox* 899, fr., July 6, 1901 (B, N); Washington County, Weiser, alt. 2200 ft., *M. E. Jones* 6548, July 5, 1899 (N).

OREGON.—Union County, a small tree, bank of Catherine Creek, alt. 3500 ft., *W. C. Cusick* 2385, m. f. fr., May 30, June 28, 1900 (N); Grant County, Prairie City, alt. 1040 m., *W. W. Eggleston* 13700, September 5, 1916 (N); Wasco County, along streams in yellow pines, near head of Warm Springs River, alt. 3000 ft., *E. I. Applegate* 2777, September 7, 1898 (N).

UTAH.—Mountains near Ogden, Hayden's Expedition, 1872 (N, sheet 26198 in part, with *S. lutea* Nutt.).

SALIX LUCIDA Muhl.—I am at a loss to understand the discussion of the distribution of this species by SCHNEIDER. In his discussion of *S. lasiandra* (p. 16) he says:

> In 1867 ANDERSSON created two new species: *S. arguta* and *S. lancifolia*. To *S. arguta* he referred his *S. Fendleriana* of 1858 as a synonym, but only "p. p." Nevertheless he cited both specimens upon which he previously based his species, and added to them in the first place a specimen collected by BOURGEAU "ad fl. Saskatchavan, prope Carlton-house." This specimen (I have not yet seen the type in Herb. K.) probably belongs to *S. lucida*, and is identical with one of BOURGEAU'S specimens from the "Saskatchevan, 1859," preserved in Herb. G. Therefore the typical *S. argenta* of ANDERSSON consists of three different things, namely *S. lucida* (Bourgeau)—.

From this it would seem that SCHNEIDER thinks *S. lucida* is represented in Saskatchewan by two collections of BOURGEAU. Under *S. lucida* he states:

> There is likewise no proof that it occurs in Manitoba, Assiniboia, Saskatchewan, northeastern Alberta, Athabasca, and the Northwest Territories as far north as Great Bear Lake. Apparently *S. serissima* and *S. lasiandra* have been taken for *S. lucida*, of which the northeasternmost locality from where I have seen material is the Hill (or Hayes) River in Manitoba (*R. Bell*, August 1880, no. 24585, fr.; O.). But it seems very rare (or represented by *S. serissima*) in these regions and in western Ontario, becoming frequent to the east of Lake Huron in southeastern Ontario and southern Quebec.

The first two sentences are contradictory. One says that there is no proof of the occurrence of *S. lucida* in Manitoba, Saskatchewan, etc. The second states that the "northeasternmost" (northwesternmost?) locality from which *S. lucida* is known by him is in Manitoba, and he cites a specimen in the herbarium of the Canadian Geological Survey. Although the writer has seen no specimens of *S. lucida* from Manitoba, there is a strong probability that it occurs in that province. *S. serissima*, however, is much more common there, at least in a narrow-leaved form.

SALIX GOODDINGII Ball.—*S. Gooddingii* Ball, BOT. GAZ. **40**: 376. *pl. 12, figs. 2.* 1905; SCHNEIDER, BOT. GAZ. **65**: 12. 1918; SCHNEIDER, Jour. Arnold Arb. **1**: 9. 1919.—*S. nigra* of numerous authors, not MARSH.—*S. nigra vallicola* Dudley in ABRAMS, Fl. Los Angeles and vicinity. 100. 1904.—*S. vallicola* (Dudley) Britton, N. A. Trees 184. *fig. 141.* 1908.

This species was described in 1905 from a single collection of immature and somewhat parasitized pistillate specimens, and at that time placed in the section LONGIFOLIAE. Not long after describing it, I was indebted to Professor W. W. ROWLEE for calling my attention to the fact that the species belonged rather in the NIGRAE, and that GOODDING'S no. 719 represented the staminate plant.

FIG. 2.—*Salix Gooddingii* Ball: large trees on levee at border of Arizona Agricultural Experiment Substation, near Yuma, Arizona, showing form produced in open growth.

Such an error would scarcely have been made if mature specimens had been in hand. In the present instance the type specimen, with its puberulent to pubescent branchlets and tomentose capsules, constitutes so striking a departure from the characters so long associated with the species of section NIGRAE, and agrees superficially so well with those of far western members of the LONGIFOLIAE, that the deception was complete. Recently the writer has studied the numerous older collections of this species as well as some more recent material. Some interesting notes on habit, size, etc., have been obtained by Mrs. AGNES CHASE and the

writer (figs. 2–4). The rather abundant material and the fuller notes now permit a complete description of the plant, as follows:

Shrub 3 mm. tall, to tree 3–9 dm. in diameter and at least 12 and probably 15 m. in height; bark furrowed, gray; branchlets straight, slender, yellowish, glabrous to puberulent, more or less shining, seasonal twigs usually densely pubescent to subpilose; bud scales small, 2–4 mm. long, color and pubescence as in branchlets.

Leaves numerous; stipules 1–3 mm. long, or 8–10 mm. long on vigorous shoots, semiclordate to subreniform or sublunate, glandular-denticulate to dentate, often densely glandular on the upper (inner) surface also (see *Ball* 1821, 2069; *Chase* 5517); petioles 3–6 mm. long, yellowish, densely pubescent to glabrate; blades linear-lanceolate, usually somewhat falcate, 8–15 mm. wide, 6–10 cm. long, commonly 8 mm. by 8 cm., on new shoots up to 2.4 by 15 cm., usually acute at base, acuminate at apex, margins finely and shallowly glandular-denticulate with about 8 teeth per cm., green or yellowish green on both sides, often pubescent or puberulent until half grown, usually glabrous at maturity or the midrib beneath permanently pubescent; veins prominent above.

Aments coetaneous, numerous, solitary, terminating lateral leafy peduncles 2–4 cm. long, and bearing 3–6 small leaves; rachis densely pubescent to pilose; scales oblanceolate to lanceolate-oblong, or the staminate obovate, occasionally toothed or even lacerate at apex, 2.5–3 mm. long, yellow, more or less densely pilose, sometimes nearly glabrous on outer apical portion, deciduous; pistillate aments (originally described from immature parasitized specimens) 3–6 or 8 cm. long, 1.5–2 cm. wide, lax; capsules ovate-conic, 5.5–7 mm. long, roughened, thinly to densely pilose with gray hairs at anthesis, becoming glabrous at maturity; pedicels 2–3 mm. long, pilose, becoming glabrous; style less than 0.5 mm. long; stigmas divided, 0.3–0.5 mm. long; staminate aments 4–6 or 7 cm. long, 1–1.2 cm. wide; stamens 5–6, filaments pilose on lower third or half.

S. Gooddingii is found along streams and about springs from southwestern New Mexico to southern Nevada (Lincoln County), Baja California, and thence northward through the interior of California to Tehama County, in

FIG. 3.—*Salix Gooddingii* Ball, showing forms produced under conditions of previous over-crowding; near Yuma Experiment Farm of U.S. Department of Agriculture, in California, near Yuma, Arizona.

the vicinity of Red Bluff. It is most abundantly distributed in the valleys, having an elevation of only 0–200 ft., but ascends the foothills streams to 1500 ft. or more. The specimens listed later are referred to this species. The arrangement is from east and south to west and north. According to SCHNEIDER, this species is found as far east as the Rio Grande Valley in south central New Mexico and in the Davis Mountains of southwest Texas. The material from those districts is discussed later.

NEW MEXICO.—Grant County, Dog Spring, *E. A. Mearns* 183 (tree 25 ft. high, 1 ft. in diam.), May 29, 190 (3?) (N); Dog Spring, Dog Mountains, *Mearns* 2419, September 22, 1903 (N); tree 20 ft. high, Emory Spring, at foot of Emory Peak, *Mearns* 277, June 4, 1902, (N); near Kingston, in meadows, at 6600 ft. elevation, *O. B. Metcalfe* 969, 1904 (N); Mangas Springs, 18 miles northwest of Silver City, alt. 4770 ft., *Metcalfe*, April 26, 1903 (N); Gila, alt. 4200 ft., *E. A. Goldman* 1561, October 9, 1908 (N).

ARIZONA.—Graham County, Sierra Bonita Ranch, 23 miles north of Willcox, *R. A. Oakley*, 1904 (B); Duncan, *J. N. Rose* 11737, April 1908 (N); Cochise County, Ft. Huachuca, *Dr. Edward Palmer* 452, April 26–May 21, 1890 (N); *Dr. Palzky* (?), 1890 (N); *T. E. Wilcox* 63, 1894 (N); Chiricahua Mountains, Joe Smith's Ranch, alt. 5500 ft., *J. C. Blumer* 2306, November 22, 1906 (B); Bonita Canyon, alt. 6500 ft., *Blumer* 2309, November 4, 1906 (B); Santa Cruz County, Nogales, *I. Tidestrom*, March 28, 1908 (B): near Santa Cruz River, east of Nogales, *Tidestrom* 743, March 30, 1908 (B): Sonaita Creek, Patagonia, *F. M. Chamberlain* 5, April 2, 1904 (N); in creek bed at Patagonia, *Tidestrom* 814, April 10, 1908; Calabases, common in bottom lands, *Tidestrom* 870, April 21, 1908 (B), same locality, *Tidestrom* 886, April 24, 1908(B); Pima County, Canoa to Arabaca (Arivaca) *D. Griffiths* 3667, March 13–April 23, 1903 (N); Tucson, *Mearns* 178 (2658) November 21, 1893 (N); *J. J. Toumey*, April 13, May 20, 1894 (N); March, May 16, 1896 (N); *Myrtle Zuck*, May 16, 1896 (N); *G. R. Vasey* 266, March 1881 (N); *J. N. Rose* 11767, April 16, 1908 (N); *Rose, Standley*, and *Russell* 15192, April 27, 1910 (N); *Blumer* B 16, alt. 2400 ft., April 15, 1907 (B); Santa Cruz River, near Tucson, *Blumer* B 16a, May 10, 1907 (B.N,); Santa Catalina Mountains, alt. 3000 ft., *Blumer* B 17, April 25, 1907 (B.N,); Santa Rita Mountains, Andrade, *Griffiths* 4079, April 18, 1903 (B.N.); Pinal County, near Dudleyville, *Griffiths* 3666, March 13–April 23, 1903 (N); Yuma County, Yuma, State Experiment Substation, *C. R. Ball* 1740, 1741, June 15, 1911 (B,N); *Ball* 1901, May 26, 1915 (B,N); Mohave County, Topock, abundant along Colorado River, alt. 600 ft., *E. A. Goldman* 2970, September 27, 1917 (N); Beaverdam, alt. 1800 ft., *M. E. Jones* 5020, April 5, 1894 (N); Littlefield, near petrified springs, *I. Tidestrom* 9236, April 29, 1919 (B); at spring 8 miles above Pierce's Ferry, alt. 1700 ft., *Jones* 5077u, April 18, 1894 (N); locality unknown, Fremont's Expedition to California, no. 202 (A), 1845 (N), has "Utah" written on label, but "Ariz." added by same hand that added number and date; Beaver Creek, *B. E. Fernow*, August 1896 (N).

FIG. 4.—*Salix Gooddingii* Ball, showing character of bark on large trees, near those shown in fig. 2.

NEVADA.—Lincoln County, Muddy Creek (R) near Virgin River, *L. N. Goodding* 689, (*type*), May 2, 1902 (B, N); Rioville, Colorado River, *Goodding* 719, May 6, 1902 (B, N); along ditches, Bunkerville, *I. Tidestrom* 9202, May 27, 1919 (B); Nye County, Ash Meadows, *Coville* and *Funston* 2145, March 1891 (N), sub nom. *nigra venulosa*.

MEXICO.—Baja California, Seven Wells on Salton River, *E. A. Mearns*, 2869 (Internat. Boundary Commission), April 8, 1894 (N); *L. Schoenefeldt* 2877 (Internat. Boundary Commission) April 9, 1894 (N).

CALIFORNIA.—Mexican Boundary, Unlucky Lagoon, *L. Schoenefeldt* 2918, May 1, 1894 (N); Imperial County, Yuma (Fort Yuma Indian Reservation) pumphouse at ferry, *C. R. Ball* 1741, June 15, 1911 (B); Indian Reservation, *Agnes Chase* 5517, April 7, 1910 (B); Salton Basin, *S. B. Parish* 8092a, June 30, 1912 (B); San Diego County, Bernardo, San Dieguito River, *L. R. Abrams* 3371, May 2, 1903 (N); Pine Valley, *E. A. Mearns* 3977, August 12, 1894 (N); Orange County, Santa Ana River, near Orange, *L. R. Abrams* 3256 (type of *S. nigra vallicola* Dudley) April 16, 1903 (N); San Bernardino County, Colton, *M. E. Jones* 3195, April 28, 1882 (N); Fort Mojave, Mojave River, *J. G. Cooper*, March 25, 1861 (N, 319845); undated (N, 319846); Inyo County, on the old Mitchell Ranch, Resting Springs Valley, alt. 525 m., *Coville* and *Funston* 262, February 6, 1891 (N); Furnace Creek Ranch house, Death Valley, *Coville* and *Funston* 469, March 24, 1891 (N); Kern County, on the Tulare Plains, about 10 miles south of Bakersfield, alt. 400 m., *Coville* and *Funston* 1236, July 13, 1891 (N); Tulare County, Hanford, *Alice Eastwood* 3846, 3851, March 24, 1914 (N); Visalia, *Eastwood* 34, May 11, 1894 (N); Madera County, Fresno River, *J. W. Congdon*, June 21, 1903 (N); powerhouse no. 1, San Joaquin River, alt. 1000 ft., *E. G. Dudley* 5, November 1911 (B); San Joaquin County, large tree, 10–18 in. diam., in Tom Payne's or Paradise Cutoff, Tracy pike, about 10 m. south of Stockton, *C. R. Ball* 1929, June 1, 1915 (B, N). Amador County, Sutter Creek, Ione, *C. H. Merriam* 4, September 15, 1905 (letter) (N); South Jackson, 1500 ft., *Geo. Hansen* 198, July 3, 1892 (N); Sacramento County, Sacramento, *L. F. Ward* 89, October 1, 1895 (N); Sacramento Valley, Wilkes Exploring Expedition 1234 (N); Lake County, bank of Cache Creek, *H. N. Bolander* 2678 (N), 1863; Clear Lake (not certainly in Lake County), *J. Torrey* 490 (N), 1865; Yolo County, near Madison, *A. A. Heller* 5419, April 29, 1902 (N); Rumsey, *C. F. Baker* 2936, May 7, 1903 (N), Butte County, Biggs, near United States Experiment Farm, *C. R. Ball* 1820, 1821 (B, N), 1822, 1824 (B), August 15, 1913; same place, *Ball* 1939 June 4, 1915 (B, N); Chico, bank of Chico Creek, *Ball* 2069, June 15, 1916 (B); Tehama County, Red Bluff, *L. E. Smith*, 596, 599, 600, March 26, 1914 (N); 668, 669, May 8, 1914 (N); Shasta County, Reed Creek, *L. E. Smith* 610, March 30, 1914 (N).

In addition to this distribution, SCHNEIDER (BOT. GAZ. **65**:12–13. 1918; Jour. Arnold Arboretum 1:9. 1919) credits *S. Gooddingii* with an eastern extension of range to central southern New Mexico and southwestern Texas

(not "northwestern," as SCHNEIDER states). The specimens so determined by him are listed later. Two chief districts are involved. The localities in Dona Ana County, New Mexico, and El Paso County, Texas, are in the Rio Grande Valley near El Paso, Texas. The Davis Mountains are some 100 miles to the southeast, forming part of the watershed between the Rio Grande and the Pecos rivers. I am by no means convinced that all of this material represents *S. Gooddingii* instead of a form of *S. nigra*.

NEW MEXICO.—Dona Ana County, on the White Sands, alt. 3700–4000 ft., *E. O. Wooton*, August 24, 1899 (N, 3 sheets, twigs brown).

TEXAS.—El Paso County, near El Paso, *G. R. Vasey*, March 1881 (N, 2 sheets); *Vasey 267*, April 1881 (N, 2 sheets); *V. Havard*, November 1881 (N); without locality, *Havard*, 1881 (N 264239); Mexican Boundary Survey, chiefly in the valley of the Rio Grande below Donana, *Parry, Bigelow, Wright*, and *Schott* 1357 (N); Jeff Davis County (probably), Fort Davis, *V. Havard*, April 1885 (N); Davis Mountains, *S. M. Tracy* 187, April 24, 1902 (N); Tom Green County, Knickerbocker Ranch, along Dove Creek, *Frank Tweedy*, May 1880 (N) (strongly suggests *S. nigra Lindheimerii* Schn.).

SALIX LAEVIGATA **araquipa** (Jepson), n. var.—*S. laevigata* forma *araquipa* Jepson, Fl. Calif. 339, 1909.—The original description by JEPSON reads as follows:

Forma *araquipa* Jepson, n. form. Small tree; one-year-old shoot with dense close tomentum; brown tuft of hairs on old wood at base of season's shoot very conspicuous; leaves reddish brown above; catkins long and dense. Arbor parva ramulis annotinis cum denso appresso tomento; valde manifestus caespes fusci pili basi horni ramuli in ligno vetere; folia rufo-fusca supra; amenta longa artaque.—Dry gulches, Araquipa Hills, Solano County, May 2–6, 1891, W. L. J.

The type came from "dry gulches, Araquipa Hills, Solano County (California), May 2–6, 1891, *W. L. Jepson*." This county lies northeast of San Francisco. I have not seen the type specimen, but an examination of the material in the National Herbarium, as well as that in my own herbarium, shows that this variety is found rather rarely in central California, but occurs commonly in the southern part of the state, comprised in Los Angeles, Orange, Riverside, San Bernardino, and San Diego counties. The vesture of the seasonal twigs, the buds, the petioles, and even the basal portion of the midrib, especially beneath, makes such a striking contrast with the glabrous and shining epidermis of the typical form that forma *araquipa* seems worthy of varietal rank. It should be noted, however, that the conspicuous tuft of brown hairs

at the base of the seasonal shoots is found on many specimens of which the shoots themselves are glabrous. The following specimens are referred to this variety:

CALIFORNIA.—Sonoma County, near Sonoma, *A. A. Heller* 5348, April 23, 1902 (N); San Bernardino County, San Bernardino, *G. R. Vasey* 265, February 1881 (N); *S. B.* and *W. F. Parish* 1204, 1881 (N); alt. 300 m., *J. B. Leiberg* 3243, 3244, both in part, April 4, 1898 (N); Los Angeles County, Rivera, *E. Braunton* 364, May 10, 1902 (N); Los Angeles River near Rivera, *L. R. Abrams* 3253, April 14, 1903 (N); San Francisquito Canyon, elevation 1500 ft., *W. M. Moore*, October 7, 1912 (B); Orange County, Santiago Canyon in Santa Ana Mountains, *V. Bailey* 1185, July 17, 1907 (N); Riverside County, Barranca, in mountains east of Pigeon Pass, *F. M. Reed* 2279, March 15, 1908 (N); San Diego County, Campo, by streams, *C. G. Pringle* 332, April 18, 1892 (N); Fall Brook, *M. E. Jones* 2870, March 25, 1882 (N); Jacumba Hot Springs, near Monument 233, *E. A. Mearns* 3245, May 20; 3322, May 28, 1894 (N); Warner's Hot Springs, *Alice Eastwood* 2589, April 9, 1913 (N).

ARIZONA.—Beaver Creek, *B. E. Fernow*, August 1896 (sub nom. *amygdaloides*) (N).

SALIX LONGIPES WARDII (Bebb) Schneider.—*S. nigra Wardii* Bebb, U.S. Nat. Mus. Bull. 22. 114–115. 1881.—*S. longipes Wardii* (Bebb) Schneider, BOT. GAZ. **65**: 22. 1918.

So far as known, this species has not been reported heretofore from any station north of the Ohio River. In the autumn of 1918, a specimen collected on the banks of the Ohio, in Perry County, Indiana, was found in a collection of Indiana willows received for identification from CHARLES C. DEAM, State Forester of Indiana. On asking his interest in getting more material, he was kind enough to visit the spot again in 1920 and make another collection. Both specimens show only the characteristic foliage, but there can be no doubt of their identity.

INDIANA.—Perry County, low bank of Ohio River about 6 miles east of Cannelton, *Chas. C. Deam* 26749, September 24, 1918 (B,D); same place, a sprawling shrub growing in crevices of rock, the branches about 3 ft. tall, probably submerged during the winter, at least, *Deam* 33220, October 1, 1920 (B, D).

The recorded northern range of the species is from Washington, D.C., northwestward up the Potomac Valley to Alleghany County, Maryland, and westward in Upshur County, West Virginia (about lat. 39° N.), and Fayette County, Kentucky (about lat. 38° N.). Neither Upshur County nor Fayette

County is near the Ohio River, although the latter is in the same latitude as Perry County, Ohio, and less than 100 miles east of it.

SALIX AMYGDALOIDES Andersson.—This species is mentioned only to note extension of its range into two states excluded by SCHNEIDER, who in the main has set very accurate boundaries for its distribution. These states are Arizona and New Mexico. These specimens bear mature ovate-lanceolate leaves, and there can be no doubt of their identity, as those of *S. Wrightii* are linear-lanceolate and shorter-petioled.

ARIZONA.—Navajo Indian Reservation, Tunicha Mountains, 7000 ft., *E. A. Goldman* 2909, August 20, 1917 (N).

NEW MEXICO.—San Juan County, near Farmington, 1550–1650 m., *P. C. Standley* 7047, July 19, 1911 (N); Navajo Indian Reservation, vicinity of Shiprock Agency, 1425 m. elevation, *Standley* 7867, August 11, 1911 (N).

These localities are in the extreme northeastern corner of Arizona and the extreme northwestern corner of New Mexico, respectively.

It may be worth noting also that the excellent survey of Indiana being made by CHAS. C. DEAM, State Forester, shows, by specimens I have seen, that *S. amygdaloides* occurs in fifteen counties in the northern third of the state (3–4 tiers of counties), and at two outposts, Henry and Marion counties in the central part of the state.

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WASHINGTON, D.C.

POLYPODIUM VULGARE AS AN EPIPHYTE[1]

DUNCAN S. JOHNSON

(WITH THREE FIGURES)

While *Polypodium vulgare* is common on rocks, may often grow on the trunks of fallen trees, or sometimes even creep a few feet up living trunks, I have not been able to find a definite report of its being really epiphytic in habit in the United States. SCHIMPER,[2] the first general student of American epiphytes or air plants, says (1888, p. 131):

> In the North American forests the shade plants of the soil would not be able, because of lack of moisture, to grow on the bark of trees. Thus the so common *Polypodium vulgare* ascends to the trees in North America, just as little as it does in central or northern Europe.

Observations made at Cockeysville near Baltimore, Maryland, latitude 39° 30′ N, shows that this polypody can grow and fruit for years as a true epiphyte, high up on the erect branchless trunks of living trees. The ferns were not growing in an unusually moist region, as was true of the epiphytic individuals of it reported by CHRIST[3] (p. 325) as growing near a waterfall as Montreux, or in the damp forests of Portugal (see also SCHIMPER 1888, p. 31). On the contrary, the trees bearing this fern in Maryland were near the top of a northward facing cliff, more than 100 feet above a small stream, and at the western end of a ravine which is about 125 yards wide at this level. Two dozen or more plants of this fern were found growing in the deep furrowed bark of six different chestnut oaks (*Quercus Prinus*). The clumps of polypody were at various heights up to 20 feet or more above the ground. Clumps of all sizes were found, showing that they had started on the tree from prothallia, and had not arisen from rhizomes that had climbed upward from the soil. With one exception they were all on the north side (between N.N.E. and N.N.W.) of single erect trunks.

[1] Botanical contribution from the Johns Hopkins University, no. 70.

[2] SCHIMPER, A. F. W., Die epiphytische vegetation Amerikas. 1888.

[3] CHRIST, H., Geographie der Farne. 1910.

The exceptional case was that of a set of several clumps on a tree which had two trunks from a point about 5 feet above the ground.

FIG. 1.—East side of forked trunk of *Quercus Prinus* (between 2 feet and 6 feet above soil) showing several clumps of *Polypodium vulgare* established as epiphytes on the bark; cards 2×5 inches in size; ×$\frac{1}{8}$.

The two forks of the trunk stood almost in a north and south line, and the crotch between them in an east and west direction. The larger clump of polypody, which bore more than forty full grown leaves, grew just below the fork on the east side of the tree (fig. 1). At 6 inches and at 2 feet below this, on the same side, were two smaller tufts of this fern (fig. 1). Both the latter evidently profited from the collection of considerable water by the fork above, part of which water was directed down the shallow grooves of the bark in which these two clumps grew. This somewhat more abundant water supply, which is likewise more constant, probably explains the presence of these tufts on the east side of the tree, while all the other clumps of this polypody seen were confined to the north sides of the trees. The other five trees on which this fern was growing had trunks that were perfectly straight and without forks or any branches for many feet above the ferns (fig. 3). There was thus no collection of rain, as in the forked trunk, but each clump of polypody was dependent entirely on the portion of water that chanced to run down the particular furrow in which it grew. The fronds of the polypody on the unbranched trunks, although barely half as large as those on the forked trunk, were quite mature, and many of them bore spores. The more favorable growing conditions on the forked tree were indicated not only by the larger size of the polypody itself, but also by the richer growth of bryophytes and lichens, which were much more abundant below the fork than above it on this tree, or than on any of the erect trunks (fig. 2).

Aside from the smaller fronds of the epiphytic polypodies, they apparently were not different from those growing on the soil. In both the rhizome was largely covered by epiphytic liverworts and lichens and sometimes by more or less humus. The external character and internal structure of the rhizome and of the leaf, even to the thickness of the cuticle and of the mesophyll of the latter, were quite alike in plants of both habitats. The roots of both epiphytic and terrestrial plants were abundant, closely matted, and thickly beset with root hairs. Many of these root hairs had one or more fungous hyphae running lengthwise through them. These hyphae could often be seen entering at the tips of the root hairs. Whether they have the function of mycorhizal fungi has not been determined.

FOOD OF EPIPHYTES.—Not only the water, which was running over the bark of the supporting tree, but also the indispensable mineral foods dissolved in it, are absorbed by the roots of the epiphytic fern. In the locality under discussion, as well as in the wet tropical forests where epiphytes are most abundant, there can be but minute traces of mineral dust from the forest-covered soil

FIG. 2.—Several clumps of polypody from near *x* in fig. 1, showing epiphytic lichens and liverworts, fruiting fronds of fern above, and young plants developed from prothallia below *x* at left; $\times\frac{2}{3}$.

blown by winds to the tree tops, to be washed down over the trunks by rains. It is evident, therefore, that the air plant is really dependent on the tree not only for support, in an advantageous position for light, but it must also rely on the tree to raise from the soil the food salts needed. In other words, the mineral-containing substances, resulting from the disintegration of bark, twigs, and leaves of the supporting tree (or perhaps a neighboring one), and

which are then washed down to the epiphyte, must first be carried above the epiphyte by the water vessels inside the tree. The epiphyte is to this extent dependent on a physiological process of the living host, the upward conduction of water, which involves a considerable expenditure of energy. The mineral food demands made upon the tree by the epiphyte are thus somewhat equivalent to those made by the "half-parasite" of its host. The chief difference is that the mistletoe exacts its quota of salts (and of water also) from within the living host, before they have been

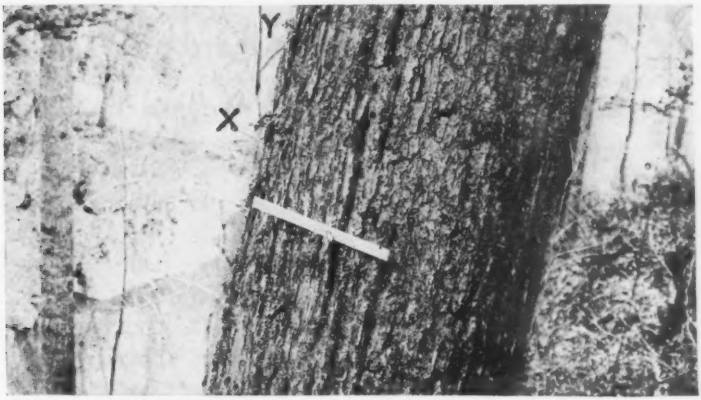

FIG. 3.—Trunk of *Quercus Prinus* bearing at *x* and *y* (north side of tree) two tufts of *Polypodium vulgare;* upper tuft 9 feet above soil, others above this are 18 or 20 feet from ground; $\times 1\frac{1}{5}$.

used by the host itself, while the air plant gets its salts from the surface of the tree after they have served their function within it. The water obtained by the epiphyte of course has never been inside the supporting tree. If the mistletoe is to be called a "water (and salts) parasite," the epiphyte is a "salts saprophyte"; that is, it secures its mineral food from the dead and no longer functional portion of the supporting plant.

ORIGIN OF TEMPERATE ZONE EPIPHYTES.—SCHIMPER (1888) announced the very important generalization that the vast majority of all vascular epiphytes are of tropical origin. Of extratropical epiphytes he believed that only the relatively few types found in

the rain forests of southern Chile and of New Zealand, with perhaps a couple of epiphyte ferns in Japan and southern Australia, are indigenous in origin. The other temperate zone epiphytes of the Old World, of South America, and according to SCHIMPER all epiphytes of temperate North America, have acquired this habit while in the tropical forest. SCHIMPER stated that it is the most xerophytic of the tropical epiphytes, those growing on the branches of the relatively dry roof of the forest, that have wandered out across the neighboring savannas and subtropical forest and onward sometimes 10 or 15 degrees beyond the tropics to populate with epiphytes the warmer and moister of the neighboring temperate forests. Because of the adaptation of these epiphytes to the dry conditions at the top of the forest, they have been able, in spite of the still more rigorous conditions encountered there, to colonize certain temperate forests. For the epiphyte that migrates from the tropics to the temperate zone, probably the most critical adverse condition encountered is not the occasional hot, dry summer, but the periods of low humidity during the generally wet winter season, when cold, dry, northwesterly winds prevail, during which the evaporation rate is high and water cannot be absorbed by the frozen roots. For example, the writer has noticed that tufts of *Tillandsia usneoides*, hung on a deciduous magnolia tree each year in May, thrive and grow rapidly during the summer, and even look fresh and green after several frosts in the autumn. They ultimately succumb, however, to the cold dry westerlies of winter, even of so moderate a winter as that of 1920–21. The precise measurement of the evaporating power of the air at these low temperatures, a factor of prime importance also to terrestrial plants, especially evergreen ones, must await the invention of a practicable frost-proof evaporimeter. Possibly the exposure of the epiphyte to sunlight, when the supporting tree is bare of leaves, is directly injurious also, although this seems hardly likely, since this same *Tillandsia* is abundant on deciduous trees only 200 miles south of Baltimore, where the winter sunlight would probably be at least as strong. The sunlight of course must work harm indirectly by increasing transpiration, which probably explains the usual restriction of polypody to the north sides of the trees.

The epiphytic ferns and seed plants of temperate North America, such as *Polypodium polypodioides*, *P. aureum*, *Vittaria lineata*, *Psilotum triquetrum* Sw. (=*P. nudum* [L.] Griseb.), *Tillandsia usneoides*, and *Epidendrum conopseum*, and the eighteen others named by SCHIMPER, have each a more or less widespread distribution in the American tropics, from whence they have probably migrated northward. The occurrence of *Polypodium vulgare* as an epiphyte in temperate North America, therefore, has a very interesting bearing on this question of the possible origin of extra-tropical epiphytes. For this fern, although distributed across the whole north temperate zone, in the New World from western Canada to Maine and south to Missouri and Georgia, and from Great Britain to Japan and southward into Northern Africa, is not known in the tropics, neither have fossils of it as yet been found there. We have no adequate evidence, therefore, that *Polypodium vulgare* acquired in the tropics the epiphytic habit which it assumes occasionally in Maryland, and more frequently in the damp forests of Portugal and Azores (SCHIMPER, 1888; CHRIST, 1910). The occurrence of this fern (or a closely similar polypody) in Cape Colony suggests that it may have crossed the equator by land, but of this there is no positive evidence, and this view seems negatived by the lack of fossils in equatorial Africa, and also by the absence of this polypody at the present day from the temperate highlands of the eastern tropics. From what is known of the habitats of *Polypodium vulgare* it seems most probable that this species is primarily a terrestrial plant of temperate forests. It probably entered North America from Eurasia via Alaska, and thence spread southward and eastward. It has acquired great hardiness while living on dry rocky ledges, often with a very scant water supply, and with no more soil than can collect in a few minute cracks of the rock. Thus this temperate zone polypody has come to be able to persist also in some shaded situations, on the very precarious supply of water and minerals to be found on the trunk of a rough barked tree. This is clearly true in spite of SCHIMPER's somewhat too positive statement (1888, p. 152) that "in the less damp North American forests the first step, the migration of the terrestrial plants to the trees, is impossible, and herewith the origin

of an indigenous epiphytic association is excluded from the beginning." This *Polypodium* seems evidently an endemic epiphyte of the temperate zone, and not one imported with this habit already formed from the tropics. It might well be designated a facultative epiphyte. In its ability to live on various substrata it closely resembles dozens of species of ferns and seed plants of the tropical forests which can be found growing, now on soil, now on dry rocks, and again as epiphytes on tree trunks.

It might perhaps be suggested that more of our temperate zone plants should prove able to live on trees. As a matter of fact, however, few of our saxicolous vascular plants are really as hardy as this polypody, the thick-cuticled leaves of which are capable of rolling up in dry weather and so of lessening transpiration. The combination of these two features, uncommon in plants of this region but common in epiphytic ferns of the tropics, is probably an important one in enabling this fern, and likewise its relative *Polypodium polypodioides*, to adopt the epiphytic habit. The evergreen leaves of *Polypodium vulgare*, which are also characteristic of most, although not of all epiphytes, are probably of great importance to this plant of shady deciduous forests. They enable it to carry on an important share of its photosynthetic work on any mild days between October and May, when abundant light reaches it because the surrounding trees are bare of leaves. In other words, while growing on soil or rocks this fern has developed more of these xerophytic characters, which fit it for living as an epiphyte, than perhaps any other vascular plant of the northeastern United States. It seems at the present time to be an indigenous temperate-zone epiphyte in the making.

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CHROMOSOMES OF CONOCEPHALUM CONICUM

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(WITH PLATES IV, V)

The discovery of visible chromosome differences between the sexes in many animals has led to a very wide acceptance of the hypothesis that sex in animals is determined by the presence or absence of certain chromosomes. This discovery has stimulated botanists also to search for sex determinants, and experimental work has apparently demonstrated that in *Sphaerocarpos* and *Thallocarpus* two of the four spores formed by the division of a spore mother cell produce male plants and the other two female plants. In several dioecious mosses also experimental results indicate that the sex potentialities are probably separated in the reduction divisions. As yet, however, a visible chromosome difference between the sexes has been found in only two species of plants, *Sphaerocarpos Donnellii* reported by ALLEN,[1] and *S. texanus* reported by Miss SCHACKE.[2]

The present study of the chromosomes of *Conocephalum conicum* (L.) Dum. was begun primarily for the purpose of determining whether or not there exists a visible difference between the chromosomes of the two sexes in this species. The results in regard to this question are totally negative, but the chromosome number is found to be nine instead of eight, as reported by previous workers for the gametophytes of this species.

The material used in the greater part of the study was grown in the greenhouse in two separate cultures of male and female plants respectively. These cultures were started with thalli bearing old gametophores of the previous season's growth, collected

[1] ALLEN, C. E., A chromosome difference correlated with sex difference in *Sphaerocarpos*. Science, N. S. **46**:466–467. 1917.

———, The basis of sex inheritance in *Sphaerocarpos*. Proc. Amer. Phil. Soc. **58**:289–316. 1919.

[2] SCHACKE, M. A., A chromosome difference between the sexes of *Sphaerocarpos texanus*. Science, N. S. **49**:218. 1919.

November 8, 1919, in Parfrey's Glen near Merrimac, Wisconsin. The archegoniophores were removed to prevent the possibility of the development of male sporelings from the sporogones, which latter were well developed at that time. The plants grew rapidly, and apical tips of the plants of the two sexes were fixed at several different times during the latter half of December. A few almost mature antheridiophores fixed in the field and imbedded in paraffin were obtained from Dr. W. N. STEIL. In addition to this material Dr. ALFRED GUNDERSEN and Professor A. F. BLAKESLEE generously supplied living plants from stock received from Copenhagen, and Professor A. J. EAMES sent plants from Cascadilla Ravine, Ithaca, New York. Comparative studies were made on these plants, but all figures shown were drawn from the Wisconsin material.

Flemming's medium solution with 4 per cent of urea added was used in fixing. Paraffin sections 4–6 μ thick in the case of the apical tips and 3 μ thick in the case of the antherids were stained with Flemming's triple combination. The sections on a few slides were restained in Heidenhain's haematoxylin, but gave results less satisfactory than those obtained with the triple stain.

The resting nuclei and stages in the formation of the spirem were not examined critically in this study. Numerous nuclei in spirem stages and in equatorial plate stages were found in these preparations, but very few cases of spirem segmented into chromosomes not yet drawn into the equatorial zone of the spindle were seen. Evidently, as observed by FARMER,[3] the transition from the unsegmented spirem stage to the equatorial plate stage is very rapid, if indeed the migration toward the equatorial region does not begin before the segmentation of the spirem, as evidenced by the frequently observed tendency of the chromosomes to lie end to end in the equatorial plate (figs. 2, 3, 9). The limited number of observations, however, does not justify any conclusion on this point.

Judging by the large number of nuclei in the equatorial plate stage, a considerable pause in the movement of the chromosomes occurs at this point, which also coincides with FARMER's observations. The longitudinal splitting of the chromosomes does not

[3] FARMER, J. B., On spore formation and nuclear division in the Hepaticae. Ann. Botany **9**:469–523. 1895.

become apparent until very late; in fact, it is perceptible only when the separation of the daughter chromosomes has actually begun (figs. 13–15). The chromosomes are in the form of bent, crinkly rods of varying lengths (figs. 1–11). The crinkliness is less apparent in the late metaphases and in the anaphases when the chromosomes are drawn out into smooth rods (figs. 12, 16, 19). As observed by ESCOYEZ,[4] they occupy a very definite plane in the equatorial plate stage; in polar view they are easily counted at this time, but in lateral view they appear as tangled masses (figs. 8, 14, 15). Only one case (fig. 11) was found of an equatorial plate stage in which the individual chromosomes could be traced with any degree of certainty in a lateral view, and a very few such cases in anaphases (figs. 12, 16, 19). The chromosome number is plainly nine in either sex (figs. 1, 2, 4, 9, and 18 female; figs. 3, 5, 6, 8, and 10 male), one of the chromosomes being very small. This small chromosome shows no constant difference in behavior from the other chromosomes, either as to its position on the spindle or in its time of division. In one case (fig. 15) it was found to have been divided earlier than the other chromosomes, and in another case it was found undivided in the equator of the spindles when the other chromosomes were in anaphase (fig. 19). Metaphases and anaphases in which the individual chromosomes are distinguishable are very rarely found, but if the small chromosome constantly led the way in division, as it appears to do in fig. 15, or if it constantly lagged, as seems to be the case in fig. 19, it should usually be visible in the metaphases and anaphases, even though the other chromosomes are not distinguishable one from another. Apparently the small chromosome ordinarily divides at about the same time as the other chromosomes, and in lateral view is distinguishable from them only in rare cases (figs. 12, 15, 16).

In cells of the apical tip of the thallus (of either sex) in which the chromosomes are commonly spread out so as to make accurate counts possible, the small chromosome is visible in about 80 per cent of the cases counted; but in the antherid, where the cells are much smaller and the chromosomes generally more closely grouped,

[4] ESCOYEZ, E., Blepharoplaste et centrosome dans le *Marchantia polymorpha*. La Cellule **24**:247–256. 1907.

it is visible in a much smaller percentage of the cases. Considering the size of this chromosome, it is to be expected that in some cases it should be obscured from vision by the other chromosomes (figs. 7, 8, 14, 17).

FARMER, BOLLETER,[5] ESCOYEZ, and WOODBURN[6] report eight chromosomes in the haploid nucleus, and in my preliminary note[7] I suggested the possibility of a variation as to chromosome number in this species. More recent studies in plants from Ithaca and from Copenhagen make it seem quite certain that the same number of chromosomes is to be found in the plants of this species in those regions. It seems probable, therefore, that these investigators have overlooked the small chromosome, a thing which might easily have happened, especially since they were interested primarily in other phenomena.

A comparison of the chromosomes of one sex with those of the other shows no perceptible difference, either in the number or size relations, as may be seen by comparing figs. 1, 2, 4, 7, 9, and 18 (female) with figs. 3, 5, 6, 8, and 10 (male). Although this condition of like chromosomes in the two sexes in *Conocephalum* is not an evidence against the sex chromosome basis of sex inheritance in the dioecious Bryophyta, it does show that the marked difference between the chromosomes of the two sexes in *Sphaerocarpos* is not a universal condition among these plants.

Summary

1. The chromosome number in the gametophyte of *Conocephalum conicum* (L.) Dum. is nine instead of eight as reported by previous investigators.

2. The chromosomes vary considerably in size, one being very much smaller than any of the other eight.

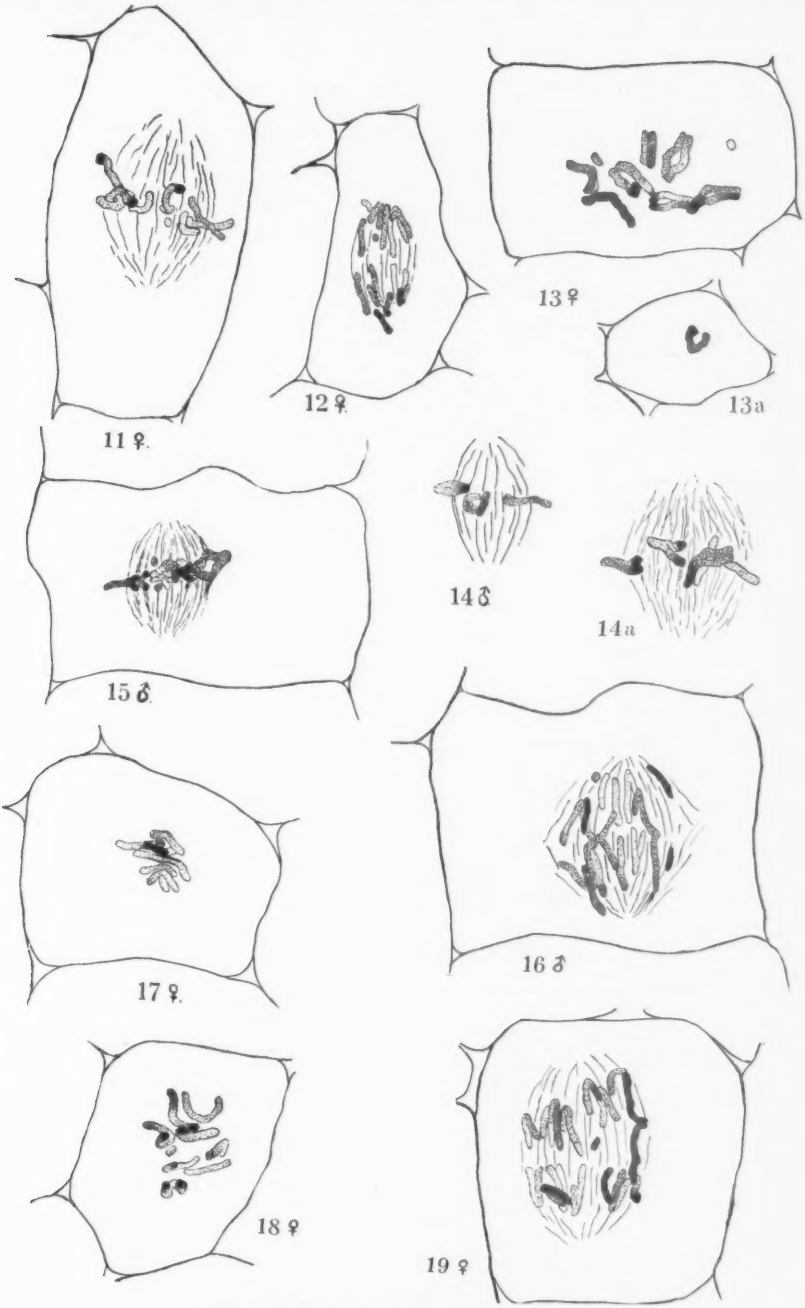
3. There is no perceptible difference between the chromosomes of the male and those of the female plant.

[5] BOLLETER, E., *Fegatella conica*, eine morphologisch-physiologische Monographie. Beih. Bot. Centralbl. **18**:327–408. 1905.

[6] WOODBURN, W. L., Spermatogenesis in certain Hepaticae. Ann. Botany **25**:299–313. 1911.

[7] SHOWALTER, A. M., The chromosomes of *Concephalum conicum*. Science, N. S. **53**:333. 1921.

SHOWALTER on CONOCEPHALUM



SHOWALTER on CONOCEPHALUM

4. The plants received from Ithaca and Copenhagen show the same number and size relations of the chromosomes as do the Wisconsin plants.

I wish to acknowledge my indebtedness and gratitude to Professor C. E. ALLEN, at whose suggestion and under whose direction this study has been made.

UNIVERSITY OF WISCONSIN

EXPLANATION OF PLATES IV, V

All drawings were made with the aid of a camera lucida at a magnification of about 3800, using a Zeiss 2 mm. apochromatic objective N. A. 1.40 and compensating ocular no. 18 with a tube length of 160 mm.

FIGS. 1–11.—Equatorial plate stages in polar view (some slightly oblique) except fig. 11 and one cell in fig. 8, which are in lateral view; symbol following number indicates sex in each case; fig. 1 from cell of dorsal surface layer near apical cell; figs. 3–6 from cells of ventral surface layer; in fig. 4 one chromosome at left upper focus cut in sectioning; figs. 7, 10, and 11 from cells of interior of thallus; fig. 8, group of six cells in antherid; fig. 9, cell of young scale.

FIG. 12.—Anaphase in cell of air chamber wall, small chromosome being visible in upper group only.

FIG. 13.—Early metaphase in cell of ventral surface layer, in slightly oblique (nearly polar) view; one chromosome, except tip of one end, in adjacent section shown in fig. 13*a*.

FIGS. 14, 14*a*.—Early metaphase in cell of interior of thallus, cut in sectioning; chromosomes not all distinctly recognizable.

FIG. 15.—Early metaphase in cell of scale, showing small chromosome already divided, other chromosomes not individually distinguishable.

FIG. 16.—Early anaphase in cell at juncture of scale and main body of thallus.

FIGS. 17, 18.—Anaphase daughter groups in successive sections of same cell, seventeen in polar view, eighteen in equatorial view; cell in floor of young air chamber.

FIG. 19.—Early anaphase in cell of ventral surface layer; small chromosome not yet divided.

PEACH YELLOWS AND LITTLE PEACH[1]

MEL. T. COOK

(WITH PLATES VI, VII)

Peach yellows and little peach are well known but poorly understood diseases, and have been the subject of study by many workers for a number of years. Although they have engaged the efforts of some of our most efficient workers, the causes are as yet unknown, the symptoms not well defined from similar symptoms due to some other common causes, and the methods of control are very unsatisfactory. Although the researches have been directed along many lines, very little attention has been given to the morphology of the organs of the infected plants as compared with the morphology of corresponding organs on healthy trees. The fact that a knowledge of the morphology is frequently a very important factor for physiological studies has led to the preparation of this paper, hoping that the accumulation of data along various lines may eventually assist some student to solve this problem.

The material used was taken from trees in an experimental orchard at Vineland, New Jersey, which was planted and managed by the Department of Horticulture of the New Jersey Agricultural Experimental Station. The trees were under constant observation, and there was no doubt as to their condition. The material was carefully collected during the early morning and mid-afternoon of a bright warm day in midsummer, when the conditions were exceptionally favorable for growth. Care was taken to select leaves of approximately the same age, and the same precaution was taken with the twigs. A great many sections were cut and a considerable number of drawings made, from which the figures shown in the plates were selected.

The studies were based on a comparison of the structure of corresponding parts, the relative amounts of starch in these organs morning and afternoon, and its relative location. The studies of

[1] Paper no. 29 of the Journal Series, New Jersey Agricultural Experiment Station, Department of Plant Pathology.

structure did not show any differences of importance, and will not receive further consideration at this time. The study, however, of the amount and location of the starch within the tissues of the leaves and green shoots gave some interesting data, and therefore the basis of the work is a comparative study of the results of photosynthesis and translocation of carbohydrates in healthy and diseased trees.

Before considering this phase of the work, the generally recognized symptoms of these diseases are indicated, since they must be referred to from time to time. The first symptom in both cases is an infolding along the midrib or rolling of the margins, accompanied by a pronounced backward curving from base to tip so as to give a sickle or crescent effect, and the development of a decidedly leathery texture which is very apparent to the touch. The second symptom for yellows is the development of enlarged, prematurely ripened fruits, which show a characteristic red spotting or blotching over the surface and through the flesh, especially prominent near the stone. The final stage in the yellows is the development of fascicled, willowy shoots. Very similar symptoms may be produced by partial or complete girdling of trunk or branch by winter injury at the collar, by borers, by label wires, or other factors. There is no doubt that many of the reported cases of peach yellows in the past were in reality cases in which the symptoms were produced by some of these causes. The first stage or leaf characters in little peach is similar to that of yellows, but is very likely to be more pronounced than in yellows. In the second stage the fruit is small and ripens later than in the normal healthy trees. There is no willowy growth as in the case of yellows. The symptoms just described are subject to many variations, dependent upon cultivation, care, and other factors. Yellow foliage may be due to many other causes, and is not necessarily a symptom of yellows. In fact, trees infected with this disease may be very green, especially if fed with a fertilizer high in nitrogen. Trees infected with yellows will sometimes persist for a number of years, but those infected with little peach usually die in a comparatively short time.

In a normal healthy plant the starch content is expected to be much greater in the afternoon than in the early morning, due to

the high photosynthetic activity during the day and the lack of photosynthesis and a very active translocation of starch during the hours of darkness. In this work a study of the sections of leaves from healthy trees removed early in the morning and in mid-afternoon was made for comparison with leaves from diseased trees which were collected at the same time. In the leaves from normal healthy trees it was found that there was very little or no starch in the leaves during the morning hours, and an abundance during the afternoon (figs. 1, 2.) This of course was to be expected, and indicated that the photosynthetic and translocation processes were normal and active on the day that the material was collected. In some instances a small amount of starch was found in the cells in the morning in the immediate vicinity of the veins (figs. 3, 4). This was no doubt due to incomplete translocation and may possibly indicate a slightly abnormal condition.

Leaves were collected from the varieties known as Stump, Hiley, and Chinese cling, which were affected with yellows. In those in which the disease was severe, the amount of starch in the sections from leaves cut in the morning was almost as great as the amount found in leaves cut in the afternoon, indicating little or no translocation of the carbohydrates (figs. 5, 6). The amount of starch, however, was not as great in either case as in the healthy Elberta (fig. 2) in the afternoon, but was greater than in the healthy Hiley (fig. 4). These differences in the amount of starch in the individual trees may be due to a difference in the physiological activities of the trees, and may possibly be accounted for by differences in variety, age, or other factors.

A morning section of a Chinese cling affected with yellows (fig. 7) compared with a morning section of a healthy tree of the same variety showed a much larger amount of starch in the leaf from the diseased tree than in the leaf from the healthy tree, indicating not only a reduced translocation of carbohydrates but also an accumulation of these products. There was very little difference, however, between the amount of carbohydrates found in the morning and afternoon sections from diseased trees (figs. 7, 8).

The little peach was studied on Elberta and Hiley. The amount of starch was practically the same in the sections from

leaves collected in the morning as in the afternoon (figs. 9, 10), but was less than in the trees affected with yellows (figs. 5, 6). In some other sections, however, the amount of carbohydrates in both morning and afternoon sections was greater than that shown in figs. 9 and 10. The starch in the sections from leaves cut in the morning was most abundant in the central part of the leaf (fig. 9), and may indicate some translocation. A morning section of leaf from Elberta infected with little peach (fig. 11) showed a large amount of starch, indicating that very little translocation of starch had taken place during the preceding night.

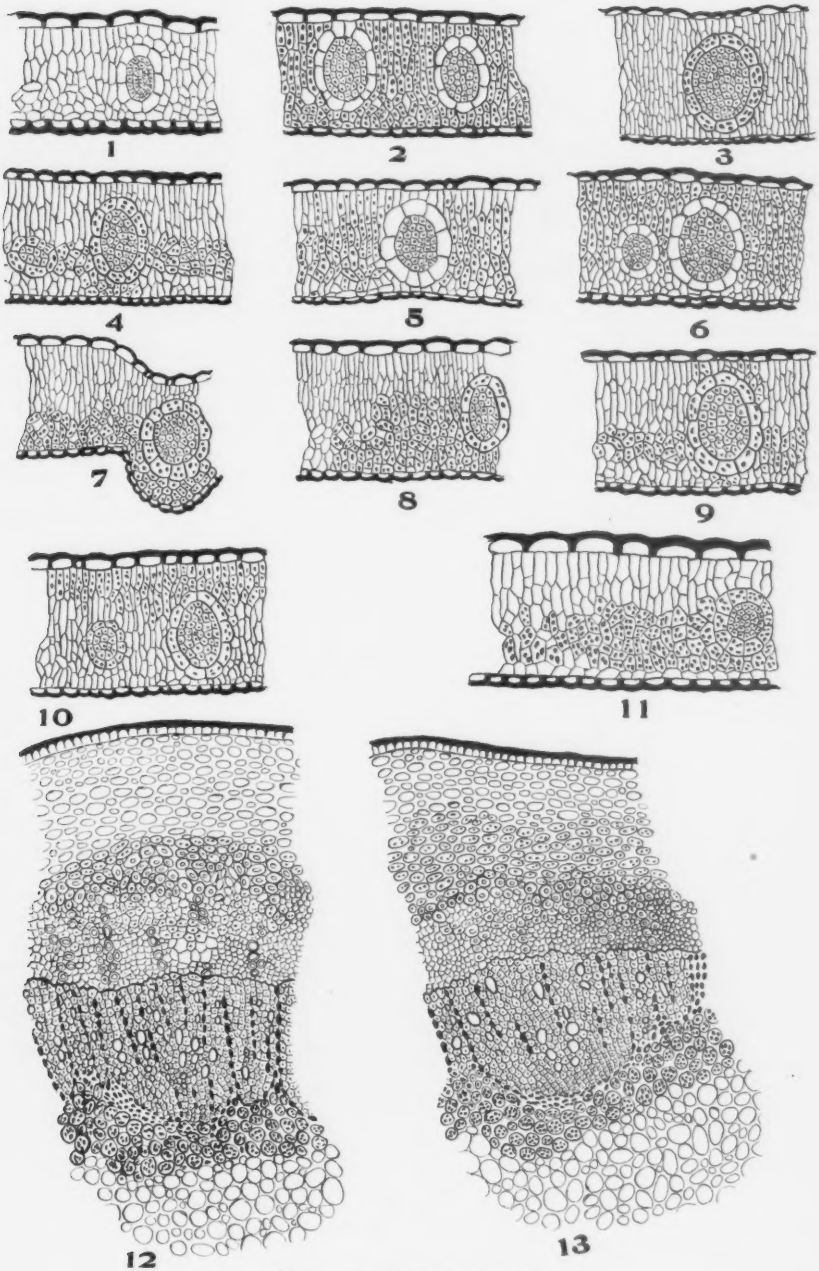
Pieces of new growth shoots were collected at the same time that the leaves and sections from Elberta, Stump, Hiley, and Chinese cling were studied. The results were practically the same throughout, but as the material from the Hiley was most abundant and most satisfactory it is used for this part of the discussion. A comparison of morning and afternoon sections of young shoots from a healthy tree shows a considerable amount of starch in the inner layers of cortex in the afternoon section (fig. 13) and very little in the morning section (fig. 12), indicating normal translocation of carbohydrates. These twigs were from the same tree as the leaves in figs. 3 and 4. The shoot from the tree affected with yellows (figs. 14, 15) was slightly older than the healthy shoot. The amount in the morning and afternoon was practically the same, indicating that there was little or no translocation of carbohydrates. These twigs were from the same tree as the leaves shown in figs. 5 and 6. The sections from the tree affected with little peach showed a slightly smaller amount of starch in the morning (fig. 16) than in the afternoon (fig. 17), which may possibly indicate that there was a small amount of translocation. These twigs were from the same tree as the leaves in figs. 9 and 10.

It will readily be seen that all these studies on both the leaves and the new growths indicate that the translocation of starch is partly or completely inhibited in the diseased trees, probably dependent upon the severity of the disease. This is indicated by the large amount of starch present in leaves and green twigs from diseased trees in the early morning, as compared with the relatively small amounts in leaves and green twigs from healthy trees at the

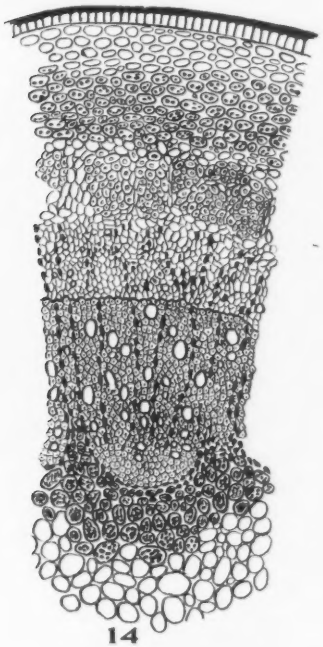
same hour. It is very generally recognized that girdling interferes with the translocation of carbohydrates, and as a result thereof bearing plants very frequently produce extra large fruits which usually ripen prematurely. The production of large premature fruits is also a characteristic symptom of yellows, and it therefore appears that the physiological behavior of a tree affected with yellows is the same or very similar (so far as photosynthesis and translocation of carbohydrates are concerned) as in a tree that has been girdled. In trees affected with little peach, however, the symptoms, so far as the fruit is concerned, are just the reverse, the fruit being somewhat smaller and ripening later than normally. This may possibly account for the fact that sections of twigs from trees affected with little peach showed some evidence of translocation of starch, while those from trees affected with yellows did not show any such evidence. These differences, however, may have been due to other causes, such as severity of infection, age of trees, or other factors.

The preceding discussion indicates that the translocation of starch is greatly reduced, possibly completely checked, in trees affected with either of these diseases; or that have been girdled and injured by label wires, bores, or at the collar as a result of freezing. In all cases the results are an accumulation of starch in the leaves, which may account for the leathery texture, but does not offer an explanation of the willowy growth of the final stage of the yellows. If the translocation of carbohydrates is reduced or prevented, however, it may have a secondary effect on the tree, resulting in the willowy growth.

Furthermore, the reduction or inhibition of the translocation of carbohydrates may also account for the enlarged premature fruit which is characteristic of trees affected with yellows, or that have been girdled, but it does not explain the undersized fruit and delayed ripening which is characteristic of trees affected with little peach. These facts indicate that some of the symptoms of these diseases are due to reduced or inhibited translocation of carbohydrates. The cause of this condition is a question that remains unanswered.



COOK on PEACH DISEASES



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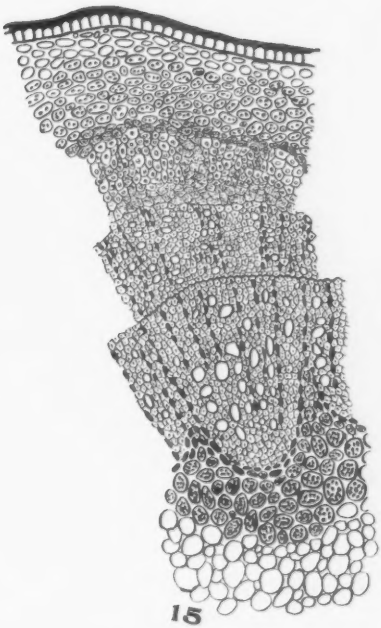

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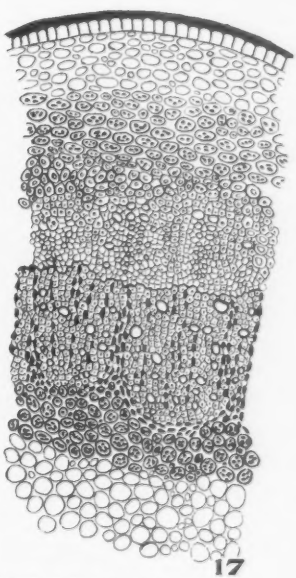

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COOK on PEACH DISEASES

EFFECT OF LOCATION OF SEED UPON GERMINATION

EDWARD N. MUNNS

The influence of parent trees upon the size and germination of Jeffrey pine seeds has been shown in a previous paper.[1] The marked results obtained from that work resulted in the present study, in which it has been sought to determine the value of seeds from different parts of the pine cone; and to decide what relation, if any, exists between the position of the seed and germination. The cones used were collected from *Pinus Jeffreyi* trees on the eastern slope of the Sierras in Lassen County, California, in September 1919. No attempt was made to choose the trees from which the cones were taken, except that the trees were young and growing thriftily, considering the site upon which they stood.

The cones were grouped according to size in three divisions, based on the gross characteristics of length, breadth, and weight. They were dried slowly in a room at air temperature, and as they opened the seeds were extracted. The cones were divided into three sections of approximately equal size, to be known as the upper, middle, and lower portions. The seeds were carefully collected and graded into three classes, large, medium, and small, using ocular means of determining the size and comparing one seed with another. Inasmuch as a number of individuals helped to determine the size of the seed grains themselves, the individual variation from this source was very largely eliminated. The seeds were cleaned, counted, and weighed, each lot kept separately, and sufficient seeds to carry out the test taken at random from each lot. To determine the germination, a number of each lot of seeds were sown in cans containing a uniform depth of soil and covered by an approximately equal depth of sand in each case. As previous work has shown that for Jeffrey pine a soil moisture content of about 15 per cent gives the best results, frequent weighings were made to keep the moisture content of the samples a constant at this figure. The result of this study is presented in tables I–VII.

[1] MUNNS, E. N., Effect of fertilization in seed of Jeffrey pine. Plant World 22:4. 1919.

It was found that there was an increase in the number of seeds with an increase in the size of the cones, medium cones having 27 per cent more seeds than the smaller ones, and the large cones

TABLE I

NUMBER AND WEIGHT OF SEED PER CONE

SIZE OF CONES	WEIGHT OF CONE (GM.)	NUMBER OF UNDEVELOPED SEEDS PER CONE	NUMBER OF DEVELOPED SEEDS PER CONE	WEIGHT OF DEVELOPED SEEDS IN CONE (GM.)	AVERAGE WEIGHT PER 100 SEEDS (GM.)						
					By portion of cone			By size of seed			Average for cone
					Upper	Middle	Lower	Large	Medium	Small	
Large	228.8	69.6	62.0	5.33	8.47	8.75	8.49	10.33	8.21	6.17	8.57
Medium	189.2	58.0	51.6	4.08	7.30	8.22	7.83	9.24	7.82	5.81	7.78
Small	145.7	37.3	38.9	2.66	6.42	7.18	7.68	7.83	6.49	6.19	7.09

TABLE II

NUMBER OF SEEDS PER CONE BY SIZE OF SEED

SEEDS	LARGE CONES				MEDIUM CONES				SMALL CONES			
	Upper	Middle	Lower	Total	Upper	Middle	Lower	Total	Upper	Middle	Lower	Total
Undeveloped	28.7	22.2	18.7	69.6	25.5	16.9	15.9	58.3	13.0	14.5	19.7	47.2
Large	4.9	10.2	3.6	18.7	6.2	6.9	1.8	14.9	13.6	1.5	2.0	17.1
Medium	13.2	16.1	6.4	35.7	7.3	14.9	5.6	27.8	6.5	2.9	4.6	14.0
Small	3.3	2.0	2.3	7.6	2.0	5.1	1.8	8.9	3.6	3.0	1.9	8.5
Total developed seeds	21.4	28.3	12.3	62.0	15.5	26.9	9.2	51.6	23.7	7.4	8.5	39.6
Total	.....	.....	.....	131.6	.....	.....	.....	109.9	.....	.....	.....	86.8

TABLE III

PERCENTAGE OF SEEDS IN CONE BY LOCATION IN CONE

SEEDS	LARGE CONES				MEDIUM CONES				SMALL CONES			
	Upper	Middle	Lower	Total	Upper	Middle	Lower	Total	Upper	Middle	Lower	Total
Undeveloped	41.2	31.9	26.9	100	43.7	29.0	27.3	100	27.5	30.7	41.8	100
Large	26.2	54.5	19.3	100	41.6	46.3	12.1	100	79.5	8.8	11.7	100
Medium	37.0	45.1	17.9	100	26.3	53.6	20.1	100	46.4	20.7	32.9	100
Small	43.4	26.3	30.3	100	22.5	57.3	20.2	100	42.3	35.3	22.4	100
Total developed seeds	34.5	45.6	19.9	100	30.0	52.2	17.8	100	59.8	18.7	21.5	100

51 per cent more than the small cones. Another interesting thing was that there were more undeveloped seeds than developed, except in the case of the small cones, where there was a slight decrease. In the large cones 47.1 per cent of the seeds were fully developed,

in the medium cones 47.0 per cent, and in the small cones 54.2 per cent. In each cone it was found that there were twice as many large as small seeds, and more medium seeds than there were large and small seeds together, except in the small cones where there was a slight decrease.

The quantity of large seeds amounted to about 30 per cent of the total in the large and medium sized cones, and 43 per cent in the

TABLE IV

PERCENTAGE OF SEEDS IN CONE BY DEVELOPMENT AND SIZE

SEEDS	LARGE CONES				MEDIUM CONES				SMALL CONES			
	Upper	Middle	Lower	Average	Upper	Middle	Lower	Average	Upper	Middle	Lower	Average
Developed	36.7	50.0	39.5	47.1	50.0	50.0	37.2	47.0	50.0	62.2	46.6	54.2
Undeveloped	63.3	50.0	60.5	52.9	50.0	50.0	62.8	53.0	50.0	37.8	53.4	45.7
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
				Total				Total				Total
Large	7.9	16.5	5.8	30.2	12.0	13.4	3.5	28.9	34.4	3.8	5.0	43.2
Medium	21.3	26.0	10.3	57.6	14.1	28.9	10.8	53.8	16.4	7.3	11.6	35.3
Small	5.3	3.2	3.7	12.2	3.9	9.9	3.5	17.3	9.1	7.6	4.8	21.5
Total	34.5	45.7	19.8	100.0	30.0	52.2	17.8	100.0	59.9	18.7	21.4	100.0

TABLE V

WEIGHT OF SEEDS IN GRAMS PER 100 SEEDS

SIZE OF SEED	LARGE CONES			MEDIUM CONES			SMALL CONES		
	Upper	Middle	Lower	Upper	Middle	Lower	Upper	Middle	Lower
Large	10.20	10.14	11.07	8.35	9.80	10.15	7.57	8.33	9.87
Medium	8.47	8.15	7.84	7.11	8.07	8.08	5.32	7.60	7.15
Small	5.92	6.41	6.32	4.81	6.37	5.30	4.20	6.20	5.43

small cones; medium seeds made more than 50 per cent of the total in the large and medium cones, and 35 per cent in the small cones; while the small seeds formed 12 to 17 per cent in the large and medium cones, and 21 per cent in the small cones.

The weight of seeds ranged from 4.20 to 11.07 gm. per hundred seeds, the average being 8.28 for large cones, 7.56 for medium cones, and 6.85 for the smallest. Using the smallest seeds as unity, the heaviest seeds in the small cones exceeded this by 135 per cent, the smallest in the medium cones was 14.5 per cent

heavier, while the largest was 141.7 per cent. The lightest seeds in the large cones exceeded the smallest seeds by 41 per cent, and the largest seeds were 164 per cent heavier than the smallest seeds.

Table VI shows that it is the size of seed rather than position in the cones which is the determining factor, there being a decided decline in the germination per cent with the size, while apparently no relation holds between position and germination. It has been shown that the weight of the seed is directly influenced by the

TABLE VI

GERMINATION PER CENT BY SIZE OF SEED AND LOCATION

Material	Large cones	Medium cones	Small cones	Average
Large seed	66.9	58.1	55.2	60.1
Medium seed	51.9	52.4	35.4	46.6
Small seed	35.2	25.5	23.7	28.1
Upper cones	51.0	38.6	35.8	41.8
Middle cones	52.7	50.7	39.5	47.6
Lower cones	50.7	46.7	39.1	45.5
Average for cones	51.5	45.3	38.1	45.0

TABLE VII

GERMINATION PER CENT BY WEIGHT OF 100 SEEDS IN GRAMS

Weight per 100 seeds	Germination per cent	Weight	Germination per cent	Weight	Germination per cent
4.0	17.5	7.0	40.5	10.0	64.5
5.0	24.5	8.0	48.5	11.0	72.5
6.0	32.5	9.0	56.5	12.0	80.5

size of cone, and this is further reflected in the germination. Charting the weight and germination, it was found that a straight line relation existed, which is expressed in table VII. A curious relation was shown in the rapidity of germination. Seeds from the lower portion of the cones completed half their germination five days sooner than seeds from the middle third of the cone, which in turn were five days earlier than seeds from the upper part of the cone. Apparently this was independent of the size of the seeds and varied with the size of the cone, the seeds from the larger cone being the more rapid. Final germination apparently did not conform to any regularity, except that the seeds from larger cones

completed their germination first, followed by the medium sized cone, the small cone seeds being last, with two weeks difference between the large and small cones.

These results have an immediate application in forestation work. So far as is known, little attention is being paid to the parentage or the condition of the seed before sowing. As pointed out previously, only seeds from thrifty trees should be used, and in the present study it appears that if it is impossible to collect only the largest cones in the field, a screening process is necessary to remove the small seeds and secure only those of large size. Studies under way show a relationship between the size of seeds and the early growth and establishment of forest tree seedlings similar to that given here, and it is believed that the "dominance" classes in the forest in a measure are an index of the size of the seed from which the tree originated. To secure the best possible forest, it is believed that forest nursery practice should be confined only to the production of trees from the heaviest and therefore largest seed.

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CURRENT LITERATURE

BOOK REVIEWS

Diseases of economic plants

The appearance of a revised edition of STEVENS and HALL's *Diseases of economic plants*[1] will be welcomed by every one interested in plant pathology. Since the publication of the first edition in 1910, so much progress has been made in the rapidly expanding field of plant pathology that a revised edition of this work will be appreciated, especially by the busy teacher and investigator.

The general plan of the book is similar to that of the first edition, although some changes have been made. The first fourteen pages are devoted to a brief summary of the history of plant pathology, the damage caused by plant diseases, and methods of prevention or cure. General diseases, such as damping off, root rot, and soil diseases, are discussed in a special section of the book. The diseases of special crops are grouped under the crop plants upon which they occur, and a chapter on tropical diseases has been added. This is followed by a chapter on fungicides and spraying apparatus, and another on soil disinfection. The bibliography contains 556 well chosen titles. Since the book is intended primarily as a text for college students, according to the author, many students, and certainly many teachers, will wish that the historical summary were more detailed. One might wish also that the damage caused by plant diseases had been discussed more fully. An account of the most serious epidemics probably would have been especially appreciated. The methods of disease prevention are grouped on the basis of more or less specific operations, such as seed treatment, the use of protective sprays and dusts, the selection of resistant varieties, and avoidance of practices which aid in the dissemination of the parasite. A brief account of quarantines possibly might have been desirable; and a more general grouping of control measures probably would seem preferable to some pathologists. The discussion of specific diseases is limited to essential facts. The economic importance, signs, general etiology, and control measures are given for all important diseases. The presentation is as detailed as could be expected in a book of such wide scope, and the literature citations direct the student to sources from which further information may be obtained.

The book is an excellent compendium of practical facts regarding plant diseases, and should be especially valuable as a reference. It is concisely written, well illustrated, and contains an extensive bibliography. It is to be hoped that the book will find its way into the hands not only of students, teachers, and investigators, but also of farm bureau advisers and the more

[1] STEVENS, F. L., and HALL, J. G., Diseases of economic plants (revised edition by F. L. STEVENS). pp. 507. Macmillan Co. 1921.

intelligent growers. STEVENS has rendered a distinct service to phytopathology by summarizing in a compact, neatly bound volume such a vast body of knowledge in an increasingly important field of applied botany.—E. C. STAKMAN.

A textbook of botany

Under the title *General Botany*, DENSMORE[2] has added to the already numerous textbooks of elementary botany whose scope and content are suitable for use in the junior college or normal school. The headings of the first two and of the last chapter in the book, The relations of plants to the environment, The form and adjustments of the plant body to the environment, and Plant associations, show that ecology has been given due emphasis. The intervening chapters are devoted to plant anatomy, physiology, and morphology in a way that seems to fit the title of the book. There is even an attempt at the beginnings of classification, with the consideration of representative species and families from the spring flora. In a word, the material is sufficiently comprehensive that in the hands of a good teacher it will furnish the basis of a good general introductory course in the subject.

There is evidence in the volume that it comes as a result of a wide experience in the laboratory and in the field. The illustrations are numerous, many are original, and several, such as those of diagrammatic life histories, are of more than usual merit. The addition of a glossary would have supplemented the usefulness of the volume.—GEO. D. FULLER

West African forests

A volume entitled "West African forests and forestry," by UNWIN,[3] late conservator of forests, Nigeria, is principally concerned with the economics of the forests of the west coast of Africa from the Senegal to the Congo River. It includes the regulations restricting the cutting of timber, the efforts at reforestation, notes on the most valuable timber trees, and summaries of forest exports. There are also chapters on The oil bean seeds and nuts of the forest; The oil palm and palm kernel industry; The forest in relation to agriculture; and A bibliography of West African forests. Considerable space is also devoted to the native names for the various trees.

The abundance and excellence of the photographs, together with the notes on the general forest conditions, furnish the ecologist and geographer with considerable data regarding the forest formation in a relatively unknown region. The index seems to be adequate and able to add to the usefulness of the volume, but the bibliography leaves much to be desired in the way of accuracy and completeness of citations.—GEO. D. FULLER.

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[2] DENSMORE, H. D., General botany. 12mo. pp. xii+459. *figs. 289.* Ginn and Co., Boston. 1920. $2.96.

[3] UNWIN, A. H., West African forests and forestry. 8mo. pp. 527. *figs. 110.* London: T. Fisher Unwin Ltd. 1920.

NOTES FOR STUDENTS

Flora of southern Illinois.—In analyzing the elements entering into the flora of the southern portion of the state of Illinois, PALMER[4] distinguishes as the most notable feature the presence of typically southern species which here reach their most northern extension. This southern element he regards not as a recent invasion, but as the remnants of a more numerous aggregation that existed here in the remote past. These species, therefore, are not extending but rather restricting their range. Two floristic formations are distinguished and named the Cairo and Mounds formations, from the towns about which they center. The former dominates the rich soils of the Mississippi and the Ohio River flood plains formerly covered with rich forests. Among the common tree species are *Taxodium distichum*, *Nyssa aquatica*, *Gleditsia aquatica*, *Fraxinus profunda*, *Liquidambar styraciflua*, *Quercus lyrata*, *Betula nigra*, *Carya laciniosa*, and many others. Among the herbaceous plants may be mentioned *Hottonia inflata*, *Triadentum petiolatum*, *Dianthera ovata*, *Spilanthes americana*, and *Mikania scandens*. The Mounds formation reaches its best development upon some low hills with gentle slopes of Cretaceous age. Its typical trees are less distinctively southern, and include such species as *Carya glabra*, *Quercus Muhlenbergii*, *Q. velutina*, *Q. Schneckii*, *Liriodendron tulipifera*, *Cercis canadensis*, and *Acer saccharum*. Upon the lower elevations the trees are large and tall, while upon the poorer soil and greater elevations of the Ozark hills not only is there a decrease in size, but there is a greater predominance of oaks and hickories, such as *Quercus velutina*, *Q. alba*, *Q. stellata*, *Carya glabra*, *C. ovalis*, and *C. alba*.

The report concludes with a list of woody plants collected. This includes not less than twelve species and varieties of *Carya* and fifteen species and eight hybrids of *Quercus*.—GEO. D. FULLER.

Seasonal changes in carbohydrates—MITRA[5] has recently published a paper on seasonal changes of carbohydrate materials in apple seedlings. Analysis has been made on one- and two-year old stems and roots and on fruit spurs, for the determination of the amount of starch, sucrose, maltose, glucose, and total sugars at intervals of fifteen days during the year. Some determinations of acidity in autumn, winter, and spring have also been made. Starch reaches its maximum amount in one- and two-year old apple stems in October and November, with a secondary increase in June. The same is true of roots. Total carbohydrates show a similar curve, reaching 44 per cent in winter. Total and reducing sugars in one- and two-year old stems and in roots increase in January and March. The author finds an increase in acidity in November,

[4] PALMER, E. J., Botanical reconnoissance of southern Illinois. Jour. Arnold Arboretum **2**:129–153. 1921.

[5] MITRA, S. K., Seasonal changes and translocation of carbohydrate materials in fruit spurs and two-year old seedlings of apple. Ohio Jour. Sci. **21**:89–103. 1921.

while the tissue is practically neutral in February and March. He states also that there is a general correlation between acidity of tissues and the relative activity of diastase and maltase as determined from amount of glucose and maltose in tissues. Maltose is most abundant when acidity is high and near the optimum for diastase. Glucose is found to increase in quantity in the late winter at a time when tissues are practically neutral, acidity being near the optimum for maltase activity. An average of eight determinations of maltose made in November, when acidity is highest, is 1.99 per cent, and an average of eight similar determinations made in March, when tissues are practically neutral, shows 1.86 per cent maltose. This difference seems too insignificant to conclude that maltose is present in larger quantities at a time when acidity is highest, especially when maltose determinations vary from 0.46 to 3 or 4 per cent. The only conclusion concerning this, in the reviewer's judgment, is that maltose is always present and in very variable amounts.—JOHN M. ARTHUR.

Ecology of the Gangetic plain.—In a paper of more than usual interest, DUDGEON[6] has included the results of his studies of a region whose ecology has been almost unknown. This part of India, lying immediately about Allahabad, has a distinctly periodic climate, with about 90 cm. of rainfall, and three distinct seasons. The rainy season, from June to the end of September, has high precipitation, high humidity, high temperature, and low insolation; the cold season, from October to the end of February, has high humidity, high insolation, but low rainfall and low temperature (mean 35° F. to 55° F.); the third or hot season, has low rainfall and humidity, but high insolation and temperature (mean 80° F.).

The existing vegetation is shown to be influenced quite as much by the biotic factors of a human population of 530 persons and 470 domestic grazing animals per square mile as by the nature of the climate. Most of the area is covered with dry meadow and thorn scrub, but it seems certain that these associations, now balanced against intense human influence, are really the retrogressive remains of a much richer climatic vegetation. The author seems to have thoroughly established his final conclusion, that "if the retrogressive influence of the biotic (human) factors were removed, the vegetation would pass through the progressively higher forest stages of (1) fully developed thorn scrub, (2) pioneer monsoon deciduous forest, and (3) climatic climax monsoon deciduous forest, a forest of considerable density and luxuriance." This forest, as shown by adjacent regions, would show *Terminalia tomentosa* and *Tectona grandis* as dominant, and would also contain *Sterculia* spp., *Bombax malabaricum, Anogeissus latifolia, Buchanania latifolia, Eugenia jambolana,* and probably *Acacia catchu* and *Shorea robusta*.—GEO. D. FULLER.

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[6] DUDGEON, WINFIELD, A contribution to the ecology of the upper Gangetic plain. Jour. Ind. Bot. 1:1–29. *figs.* 9. 1920.

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